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NATAL AND BREEDING DISPERSAL IN BARN OWLS

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ABSTRACT.—I studied dispersal of the Barn Owl (*Tyto alba*) in northern Utah from 1977–96. Based on 144 recoveries of 2085 banded nestlings, the average dispersal distance was 102.9 km (median = 60 km, range = 0–1267 km), occurred in most compass directions from natal sites, but was not random with mountains, deserts, and the Great Salt Lake altering dispersal routes. Dispersal distance was not correlated with severity of winter weather nor population density. Among owls banded as nestlings and recaptured as breeders, females ($N = 48$) moved significantly farther ($\bar{x} = 61.4$ km, median = 57.5 km, range = 0–160 km) than males ($N = 34$, $\bar{x} = 35.7$ km, median = 14.7 km, range = 0.8–120 km, $P = 0.015$). Turnover of breeders at nest sites resulted mostly from individuals dispersing into the study area. Only 19 (of at least 500) breeders moved from one breeding site to another. The mean distance moved between breeding sites of 2.3 km (median = 2.25 km) was not significantly different between males and females ($P = 0.9$), but more females (16) than males (3) made these moves. Eight of the adults that shifted breeding sites did so in the same year either after a failed first attempt (2) or to produce a second brood (6). The remainder changed nest sites in subsequent years.

KEY WORDS: *Barn Owl; Tyto alba; breeding dispersal; long-term study; natal dispersal; Utah.*

Dispersión natal y reproductiva de *Tyto alba*

RESUMEN.—Estudí la dispersión de *Tyto alba* en el norte de Utah desde 1977–96. Con base en 144 recapturas de 2085 pichones anillados, encontré que la distancia de dispersión fue de 102.9 km (media = 60 km, rango = 0–1267 km), ocurridas en todas las direcciones desde el sitio de nacimiento. Esta situación no ocurrió al azar en montañas, desiertos y el Great Salt Lake los cuales alteraron las rutas de dispersión. La distancia de dispersión no estuvo correlacionada con la severidad del clima invernal, ni con la densidad poblacional. Entre las lechuzas anilladas como pichones y recapturadas como reproductores, las hembras ($N = 48$) se movilizaron significativamente mas lejos ($\bar{x} = 61.4$ km, media = 57.5 km, rango = 0–160 km) que los machos ($N = 34$, $\bar{x} = 35.7$ km, media 14.7 km, rango = 0.8–120 km, $P = 0.015$). El regreso de los reproductores a los sitios de los nidos, fue el resultado de individuos dispersados dentro del área de estudio. Sólo 19 (de por lo menos 500) reproductores se movizaron de un sitio de reproducción a otro. La distancia promedio recorrida entre los sitios de reproducción fué de 2.3 km (media = 2.25 km). Esta distancia no fue significativamente diferente entre machos y hembras ($P = 0.9$). Mas hembras (16) que machos (3) hicieron estos movimientos. Ocho de los adultos que cambiaron sus sitios de reproducción lo hicieron en el mismo año despues de fracasar en un primer intento (2) o para producir una segunda nidada (6). El resto cambió el sitio del nido en los años subsecuentes.

[Traducción de César Márquez]

The Barn Owl (*Tyto alba*) is among the most widespread of land birds, and although some as-

pects of its biology closely resemble other owls (e.g., trophic biology), other attributes are strikingly different. Among the important disparities are aspects of the Barn Owl's reproductive biology and life-history (Marti 1997). Here, I show that dis-

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persal in Barn Owls conforms with the species' r-selected life-history strategy (reproduction at an early age, short reproductive life, high reproductive output, and an ability to find new resources—sometimes at great distances—through natal dispersal), but also fits some patterns of dispersal that are widespread in other birds.

Dispersal is a very important but poorly understood element of population biology (Begon et al. 1990). Dispersal may be either natal—the one-way movement by an individual from its birthplace to a breeding (or potential breeding) site, or breeding—the movement by adults between breeding sites. Natal dispersal usually covers greater distances than breeding dispersal (Greenwood and Harvey 1982). Advantages attributed to natal dispersal include reducing the chance of inbreeding, reducing competition, and extending the range (Greenwood 1983, Swingland 1983). In many bird species, dispersal patterns differ between adults and juveniles and between males and females (Greenwood 1983, Greenwood and Harvey 1982).

Relatively few studies of dispersal have been conducted on raptors. See for example, Newton (1979) and references within, Newton (1986) and Ferrer (1993) for European diurnal raptors, and Korpimäki et al. (1987), Korpimäki (1988), Korpimäki and Lagerström (1988), and Coles and Petty (1997) for European owls. In North America, see Jacobs (1995), Woodbridge et al. (1995), Steenhof et al. 1984, and Miller and Smallwood (1997) for diurnal raptors, and VanCamp and Henny (1975), Adamcik and Keith (1978), Marks (1985), Bull et al. (1988), Belthoff and Ritchison (1989), Ganey et al. (1998), Gehlbach (1994), and Arsenault et al. (1997) for owls.

Dispersal in Barn Owls has been studied in North America (Stewart 1952), Europe (Frylestam 1972, Schönfeld 1974, Glutz von Blotzheim 1979, Bairlein 1985, Baudvin 1986, Chanson et al. 1988, Taylor 1994, Martínez and López 1995), and to a very minor extent in Australia (Purchase 1972). Only Taylor (1994) presented data on both the dispersal of nestlings to breeding sites and movements of adults between nest sites.

Previously, I documented the reproductive pattern (Marti 1994) and lifetime reproductive success (Marti 1997) in a Barn Owl population breeding close to the northern limit of its range. Here, I present dispersal patterns in the same population, test whether sex and age differences in dis-

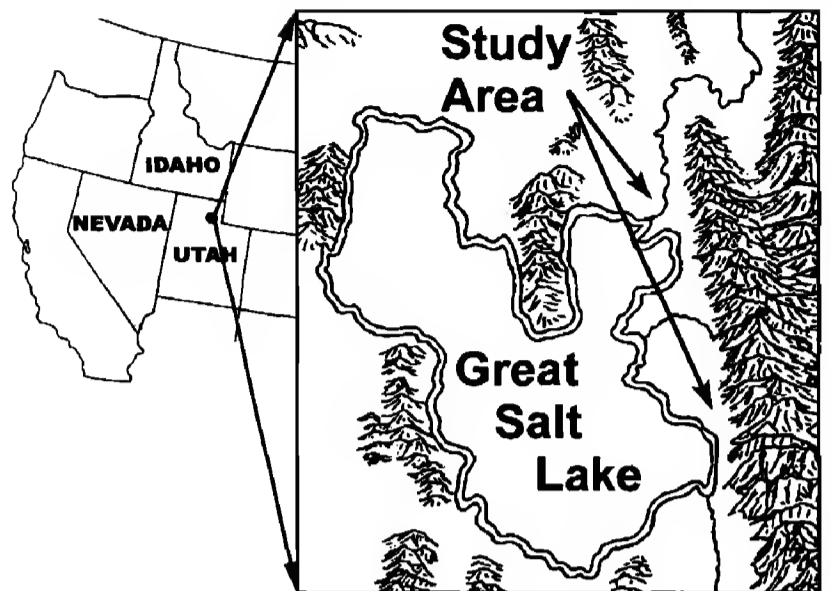


Figure 1. Location and topographic features of Barn Owl study area in northern Utah.

persal occurred and look for support that dispersal reduces inbreeding.

STUDY AREA AND METHODS

The study area was a narrow (12–25 km wide, 500 km²) valley lying between the Wasatch Mountains and the Great Salt Lake in Box Elder, Weber, and Davis counties of northcentral Utah (Fig. 1) that is close to the Barn Owl's northern range limit in the Intermountain Region (Marti 1992). The area was shrubsteppe desert but that community has been entirely supplanted by irrigated agriculture and urban development. Hot dry summers and cold winters characterize the region; mean temperatures for July and January are 23.9°C and −3.5°C, respectively.

Barn Owl nesting habitat is limited and disjunct in this area; most Barn Owls nest in lower elevation valleys where irrigated agriculture occurs. Rugged mountains and high elevation valleys immediately east of the study area were unsuitable Barn Owl habitat, and, likewise, the Great Salt Lake and alkali deserts to the west of the study area offered little habitat for Barn Owls. See Marti (1994) for more details on the study area and owl nest sites.

Most of the Barn Owls on my study area nested in nest boxes (Marti et al. 1979). From 1977–96, I visited these nest boxes year-round at least once per month. I made additional visits as needed to band and color mark nestlings and adults with a standard USGS aluminum band and a combination of colored plastic bands unique to each bird (two bands per leg) permitting identification of individuals without having to recapture them. Few other suitable nest sites existed on the study area, but owls occasionally nested in buildings and hay stacks. These were often reported to me by farmers or by owners of buildings having various problems caused by the nesting owls. Thus, I was able to document nesting in these sites as well.

I attempted to capture all breeding owls each year to determine their identity, age, and movements. Most females and some males were caught by hand in nest boxes but, because males were less often found in nest boxes, I sometimes used nest-box traps to capture them (Sau-

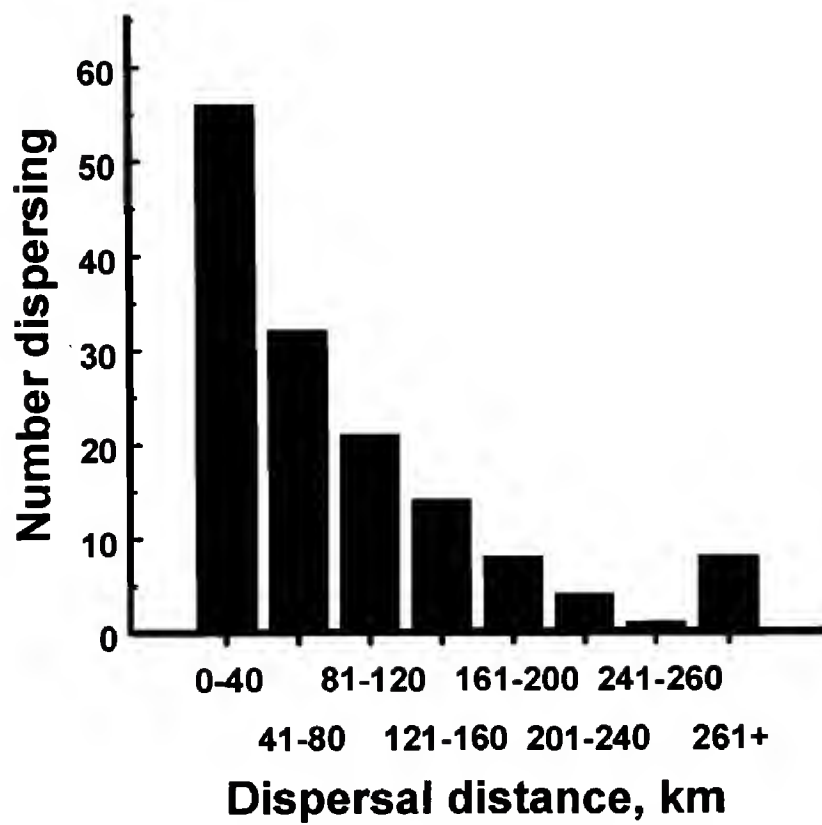


Figure 2. Dispersal distances in Barn Owls banded as nestlings in northern Utah.

rola 1987). For breeding owls not banded as nestlings, age was determined by wing-molt pattern. Barn Owls do not molt any primaries until 13 months of age (P. Bloom pers. comm., Lenton 1984, Taylor 1993). Thus, in the spring, breeding owls with one generation of primaries are in their first year of life, and those with two generations of primary feathers are at least 2-yr old. I also included data from some nestling owls that I banded on a site similar to my study area located in Cache County, Utah. Similarly, I used data from several Barn Owls banded as nestlings by the Utah Division of Wildlife Resources in Utah County, Utah and recaptured in my study area. Barn Owls were nonmigratory in northern Utah as they appear to be in most if not all other parts of the species' range (Schneider 1937, Cramp 1985, Taylor 1994).

Statistical analyses (*t*-tests and linear correlation) were performed using the Statistical Analysis System (SAS Inst. 1988). Rayleigh's test was used to check for uniformity in direction of owl dispersal after the data were transformed into unimodal data (Zar 1984). Alphas for all tests were 0.05 and all tests were two-tailed.

RESULTS

Natal Dispersal. I banded 2085 nestlings (locals in USGS Bird Banding Laboratory terminology), 384 breeding adults (adults) and 161 fledglings (hatch year) from 451 nesting attempts by at least individual Barn Owls. To exclude birds that may have died before completing their dispersal, only those that were recovered >6 mo after fledging or after they began breeding were included in the following analyses.

Of those banded as nestlings, 144 (6.9%) were

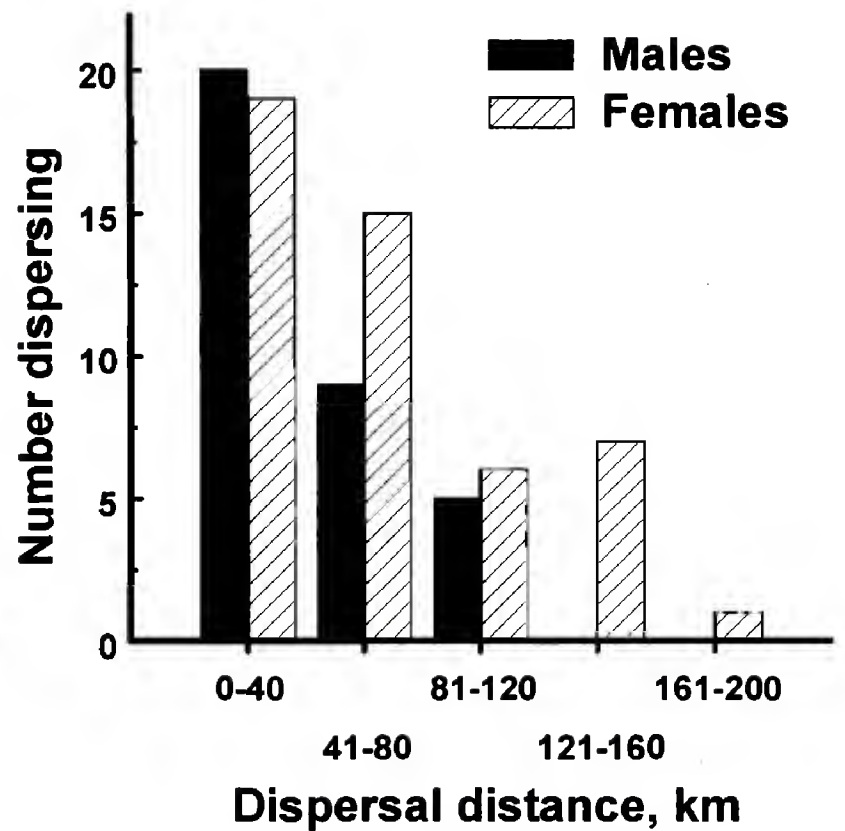


Figure 3. Comparison of dispersal distances between breeding male and female Barn Owls banded as nestlings in northern Utah.

recovered (either found dead or identified alive) at an average of 102.9 ± 162.03 (\pm SD) km from their natal sites (median = 60 km, range = 0–1267 km; Fig. 2). Among owls banded as nestlings and recaptured as breeders, females ($N = 48$) moved significantly farther ($\bar{x} = 61.4 \pm 52.04$ km, median = 57.5 km, range = 0–160 km) than males ($N = 34$, $\bar{x} = 35.7 \pm 36.61$ km, median = 14.7 km, range = 0.8–120 km; $t = 2.48$, $df = 80$, $P = 0.015$, power = 0.66; Fig. 3). One female nested in her natal site and two siblings that dispersed only 8 km from their natal site paired and raised young.

Sixty-two owls banded as nestlings were found dead off the study area at distances of 7–1267 km ($\bar{x} = 171.98 \pm 223.63$ km, median = 109 km) from their natal sites. Sex was determined for only 17 of these and dispersal distances were not significantly different between sexes in this small sample (female, $N = 8$, $\bar{x} = 93.5 \pm 63.5$ km, median = 110.3, range = 7–167 km; male, $N = 9$, $\bar{x} = 94.2 \pm 90.44$ km, median = 52, range = 7–221 km; $t = 0.02$, $df = 15$, $P = 0.98$, power = 0.98).

Owls dispersed in all compass directions from their natal sites (Fig. 4), but the pattern of dispersal direction was not random (Rayleigh's $z = 38.43$, $P < 0.0005$, $N = 82$). The local topography (Fig. 1) caused many owls to move either to the north, northwest or to the south, southeast. Those

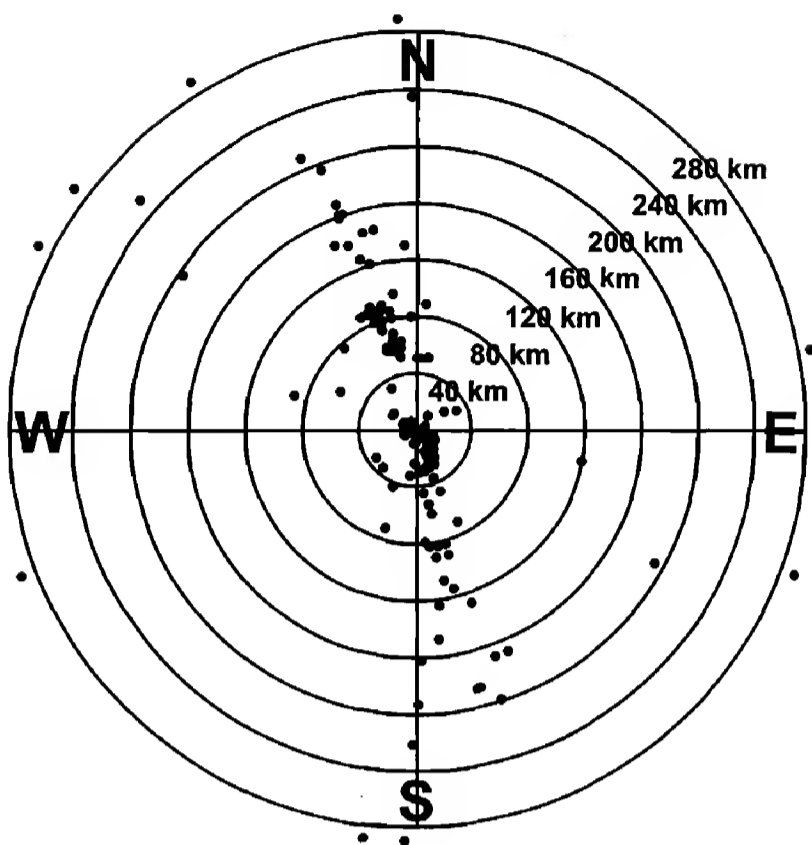


Figure 4. Direction and distance of natal dispersal in Barn Owls in northern Utah.

that moved beyond the local topographic features dispersed in all directions (Fig. 5). No relationship was found between the year of fledging and the distance of dispersal ($r = -0.08$, $P = 0.37$, $N = 135$, power = 0.54). Likewise, the severity of a winter (based on ambient temperature and depth and persistence of snow cover) was not significantly correlated with dispersal distance ($r = 0.07$, $P = 0.42$, $N = 137$, power = 0.47). Population density on the study area did not appear to be a factor either; even though numbers of fledglings varied greatly among years (Marti 1994), the number fledged in a year was not correlated with the distance of dispersal ($r = -0.01$, $P = 0.89$, $N = 18$, power = 0.89). The distance moved from natal site to breeding site was not significantly correlated with lifetime breeding success in a 19-yr interval (success = number of young fledged in lifetimes [Marti 1997]; $r = 0.11$, $P = 0.32$, $N = 82$, power = 0.70).

Unbanded birds that became breeders on my study area provided a measure of dispersal into the area. On average, turnover of breeders at nest sites was 48.1% (range = 21.4–75.0%/yr), mostly individuals dispersing into the study area. Only 23.3% of first-time breeders had been banded as nestlings on the study area (range = 0–93.8%/yr). The remaining 76.7% (range = 6.2–100%/yr) were unbanded, apparently having been raised outside the study area (Fig. 6). The nearest known breeding

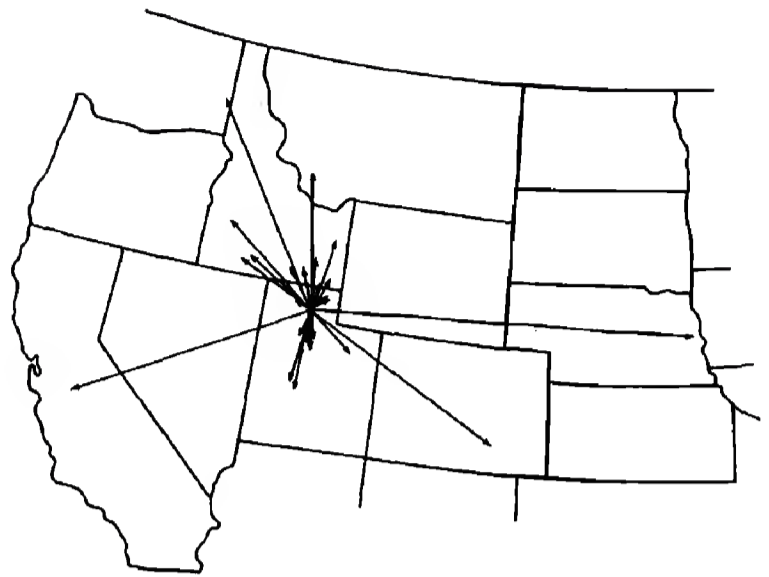


Figure 5. Long-distance natal dispersal by Barn Owls banded as nestlings in a northern Utah population.

populations were 100 km to the south and >100 km to the north and northwest.

Breeding Dispersal. Nineteen of at least 500 breeders dispersed from one breeding site to another. The mean distance moved between breeding sites, 2.28 ± 1.77 km (median = 2.25, range = 0.1–6.2 km), did not differ significantly between males and females, but >5 times as many females made those moves (female, $N = 16$, $\bar{x} = 2.3 \pm 1.63$ km, median = 2.3, range = 0.1–6.2 km; male, $N = 3$, $\bar{x} = 2.17 \pm 2.87$ km, median = 0.5, range = 0.5–5.5 km; $t = 0.12$, $df = 17$, $P = 0.90$). Eight of the adults shifted breeding sites in the same year either after a failed first attempt ($N = 2$) or to produce a second brood following a successful first one ($N = 6$). The others changed nest sites in subsequent years.

DISCUSSION

The natal dispersal that I observed followed a pattern similar to that seen in other Barn Owl populations (Taylor 1994) with young dispersing soon after fledging and making one-way movements in any direction from the natal site subject to geographic constraints. Distances were usually about 60 km but the longest exceeded 1000 km. Adults, in contrast, tended to be sedentary, rarely moving far from their breeding sites.

Stewart (1952) analyzed all banded Barn Owls recovered to 1950 in the U.S. Nestlings banded south of 35°N were all recovered within 144 km of the banding site. Those banded north of 35°N moved farther: 61% moved >80 km, 28% >320 km and 1% >1600 km. Dispersal, even in the north, was in all directions. Other Barn Owls have been

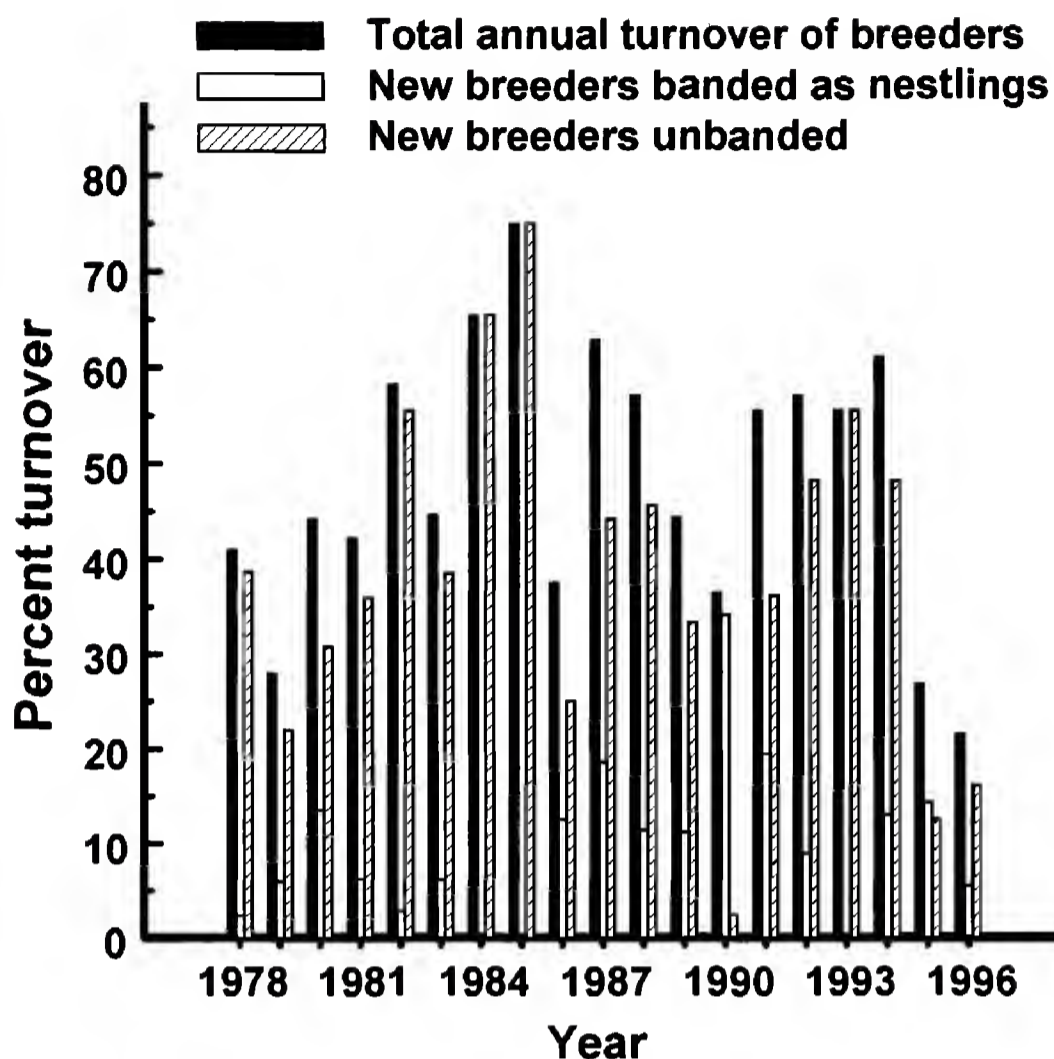


Figure 6. Annual turnover rates of breeding Barn Owls in northern Utah.

recovered in the U.S. after the 1950s over >1000 km from their banding sites (Broun 1954, Mueller and Berger 1959, Bolen 1978, Soucy 1985).

In the United Kingdom, natal dispersal was relatively short; only one individual banded as a nestling in Scotland moved >20 km to a breeding site (Taylor 1994) and the longest dispersals were <200 km (Bunn et al. 1982). In continental Europe, dispersals >1000 km were reported from Barn Owl populations in France (Baudvin 1986) and Switzerland (Glutz von Blotzheim 1979). Over 50% of nestlings banded in Germany bred at distances <50 km from their site of birth, but 24% were recovered at distances >100 km (Bairlein 1985); movements were shorter in high vole years than in low vole years (Schönfeld 1974). In Spain, natal dispersal covered significantly greater distances than did breeding dispersal (Martínez and López 1995). Natal dispersal occurred in all compass directions in Europe, even in Scandinavia (Frylestam 1972) which, like Utah, is at the northern edge of the Barn Owl's range. In Australia, two nestlings were recovered 250 and 840 km from their nests (Purchase 1972).

Dispersal studies of other raptors reveal many

similarities. Newton (1979) noted that numerous diurnal raptors in Europe rarely dispersed >50 km and that females dispersed farther than males. The most comprehensive study of dispersal in a diurnal raptor was Newton's (1986) study on the Sparrowhawk (*Accipiter nisus*). Female Sparrowhawks dispersed significantly farther from their natal areas than did males and both sexes moved in all directions. Most of the natal dispersal occurred in late summer, and population density did not seem to affect dispersal. Dispersal distances were shorter than in Barn Owls (<1–265 km) and 75% settled within 20 km of their natal site. Newton did not record any inbreeding in Sparrowhawks. Breeding dispersal by Cooper's Hawks (*Accipiter cooperii*) also resembled the pattern I found in Barn Owls. Male Cooper's Hawks did not change breeding sites, but a few females moved short distances to new sites (Rosenfield and Bielefeldt 1996).

American kestrels (*Falco sparverius*) in Florida dispersed out of their natal territories but distances were short (71% were <8 km) and the sexes did not differ significantly in distance (Miller and Smallwood 1997). In Wisconsin, natal dispersal by kestrels was much greater and males dispersed far-

ther than females (Jacobs 1995). Natal dispersal was not sex-biased in Lesser Kestrels (*Falco naumanni*) and 57% settled to breed in their natal colonies. Those that dispersed moved on average only 18.5 km (Negro et al. 1997). Swainson's Hawks (*Buteo swainsoni*) moved on average just 8.2 km (0–18.1 km) between natal and breeding sites and distances were not significant between the sexes (Woodbridge et al. 1995). Natal dispersal in a small sample of Ospreys (*Pandion haliaetus*) averaged 441 km (Johnson and Melquist 1991).

Dispersal in owls has not been well documented, but most other species appear to move shorter distances in natal dispersal than do Barn Owls. Median distance moved by radio-tagged Eastern Screech-Owls (*Otus asio*) from natal sites was only 4.4 km (0.4–16.9) (Belthoff and Ritchison 1989). Also in Eastern Screech-Owls, Gehlbach (1994) recorded a mean natal dispersal of 3.2 km, but VanCamp and Henny (1975) gave 32 km as the mean natal dispersal distance. However, about half of their birds dispersed <16 km. Mean dispersal by Great Gray Owls (*Strix nebulosa*) was 18.5 km (7.5–32; Bull et al. 1988), but Tengmalm's Owls (*Aegolius funereus*) in Finland dispersed on average 55–70 km (0–320 km) depending on the stage of the vole population cycle (Korpimäki and Lagerström 1988). Great Horned Owl (*Bubo virginianus*) fledglings from northern populations moved up to 1305 km from their nests but 53% were recovered within 25 km (Adamcik and Keith 1978). A few male Long-eared Owls (*Asio otus*) were known to nest within 2.0 km of their natal nest, but females apparently dispersed farther than males before nesting (Marks et al. 1994). Dispersal in Spotted Owls (*Strix occidentalis*), despite recent intense study of the species' biology, is poorly known. Arsenault et al. (1997) and Ganey et al. (1998) radiotracked fledgling Mexican Spotted Owls to distances of 2.1–73.5 km, but only one individual was tracked to a breeding territory at 5.8 km from its natal site. Dispersing juvenile Northern Spotted Owls were tracked from 20–98 km, but none were traced to a breeding territory (Gutiérrez et al. 1985).

Distance and direction of the natal dispersal I found in northern Utah were effective in reducing inbreeding. The only known inbreeding in my population occurred when dispersal distance was short and siblings from the same brood paired and raised young. Another female bred in her natal site but her mate was not identified. Shaw and Dowell (1989) found one instance of pairing between sib-

lings that moved only 5.4 km from their natal site, and another between a mother and son. Incest and close inbreeding have been reported only rarely in other raptors (VanCamp and Henny 1975, Bowman et al. 1987, James et al. 1987, Postupalsky 1989, Millsap and Bear 1990, Rosenfield and Bielefeldt 1992, Taylor 1994, Gutiérrez et al. 1995, and Carlson et al. 1998). It is not clear whether this low level of reported inbreeding is due to the difficulty of detecting it or to a truly low level of occurrence.

Natal dispersal may aid in range expansion and repopulation of areas where extinction has occurred. The Barn Owls' ability for long-distance dispersal coupled with their versatility in nest-site and foraging habitat have permitted them to expand their range particularly in response to human-caused habitat changes (Brown 1971, Reese 1972, Stewart 1980, Lenton 1985, McLarty 1995). Barn Owls probably did not nest on my study area until humans provided nesting places (buildings) and increased food availability through irrigated agriculture.

Even though I document long-distance movements by Barn Owls out of my study area, I do not have any data on the reproductive success of those individuals. However, several individuals that were banded as nestlings made long-distance movements out of my study area and were recovered several years later (one 12-yr old), making it likely that they did reproduce. Martínez and López (1995) considered long-distance dispersal by Barn Owls in Spain to be a disadvantage, and Newton and Marquiss (1983) showed that reproductive success for Sparrowhawks that dispersed furthest was less than those that moved shorter distances. I have considerable data on reproduction by individuals dispersing into my area, but no knowledge of the origin of most of them.

Dispersal may also speed the flow of genes among breeding populations, but almost nothing is known about this in Barn Owls or other raptor species. McLarty (1995) compared genetic similarity among three Barn Owl populations in British Columbia, northern Utah and southern California, and found sufficient genetic differences to suggest that little gene flow occurs between these populations. Utah and California populations were more similar to each other than the British Columbia population was to either suggesting more east-west than south-north movement by dispersing owls. The British Columbia population is at the north-

ern limit of the species' range and is of relatively recent origin.

My results offer little evidence that natal dispersal relieves competition because I have reproductive data only on birds that moved relatively short (for Barn Owls) distances between natal and breeding sites. I was able to show that lifetime reproductive success was not related to distance of dispersal up to the dispersal distances I was able to track, and that dispersal distance was not related to population density.

Dispersal in Barn Owls in northern Utah conformed to the patterns seen in many birds with natal dispersal covering much greater distances than breeding dispersal, and females dispersing farther than males. Natal dispersal apparently was effective in reducing inbreeding, because the distance and randomness of the direction of natal dispersal made pairings by close relatives unlikely.

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DIETS OF BREEDING PEREGRINE AND LANNER FALCONS IN SOUTH AFRICA

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ABSTRACT.—The diets of breeding Peregrine (*Falco peregrinus*) and Lanner (*F. biarmicus*) Falcons in South Africa were determined from the analysis of prey remains collected at nest sites and through direct observations to determine the regional variation in Peregrine Falcon prey and to measure diet overlap, and the potential for competition between Peregrine Falcons and sympatric congeners. Direct observations suggested that remains under-sampled small prey by about 10% and over-sampled large prey by about 8%. Peregrine and Lanner Falcons preyed mostly on birds. Pigeons and *Streptopelia* doves comprised the bulk (38–66% by frequency; 68–85% by mass) of the Peregrine Falcon prey in each of three study areas. Columbids were supplemented by starlings (mostly European Starling [*Sturnus vulgaris*]) on the Cape Peninsula, sandgrouse (*Pterocles* spp.) and swifts (*Apus* spp.) on the Orange River, and mousebirds (*Colius* spp.) in the Soutpansberg. Cape Peninsula Peregrine Falcons had the least diverse diet, the narrowest feeding niche and they took the largest proportion of juvenile birds. Peregrine Falcons on the Orange River had the broadest feeding niche and preyed mainly on ‘commuter’ species rather than sedentary residents. Lanner Falcons in the Soutpansberg took mainly terrestrial or cursorial species, particularly young chickens (*Gallus gallus*, 40%; 37%) and charadriids, but columbids were also important. The diets of sympatric Peregrine and Lanner Falcons overlapped by about 35%. Peregrines Falcons concentrated their foraging on woodland and cliff-dwelling prey, while Lanner Falcons took mainly open-country species. Close-neighboring pairs of congeners did not obviously affect the food-niche parameters of either species suggesting that they were not actively competing for food.

KEY WORDS: *Peregrine Falcon*; *Falco peregrinus*; *Lanner Falcon*; *Falco biarmicus*; *diet*; *niche dimensions*; *competition*.

Dieta de *Falco peregrinus* y *Falco biarmicus* en reproducción en Suráfrica

RESUMEN.—Las dietas de *Falco peregrinus* y *Falco biarmicus* en reproducción en Suráfrica fueron determinadas a partir del análisis de restos de presas recolectados en los sitios de anidación y a través de observaciones directas para determinar la variación regional en las presas de halcón peregrino, medir su coincidencia y la competencia potencial entre halcones peregrinos y sus congéneres simpátricos. Las observaciones directas sugirieron que las presas pequeñas fueron subvaloradas en un 10% y que las presas grandes fueron sobrevaloradas en un 8%. Los halcones peregrinos y lanarios se alimentaron mas que todo de aves. Palomas y otras aves del género *Streptopelia* representaron la mayoría (38–66% de la frecuencia; 68–85% de la biomasa) de las presas de los halcones peregrinos en cada una de las tres áreas de estudio. Las Columbiformes fueron suplementadas por *Sturnus vulgaris* en la Península del Cabo, *Pterocles* spp. y *Apus* spp. en el Río Orange y *Colius* spp. en el Soutpansberg. Los halcones peregrinos de la Península del Cabo tuvieron la dieta menos diversa y el nicho alimenticio más restringido cazando aves juveniles. Los halcones peregrinos del Río Orange tuvieron el nicho alimenticio más amplio y depredaron en “especies pasajeras” contrario a las sedentarias. Los halcones lanarios en el Soutpansberg se alimentaron de especies terrestres particularmente de pollos. (*Gallus gallus*, 40%; 37%) y Charadriiformes, las Columbiformes fueron también importantes. Las dietas de los halcones peregrinos y lanarios simpátricos coincidió en un 35%. Los halcones peregrinos concentraron su forrajeo en presas de bosques y riscos mientras que los halcones lanarios simpátricos coincidió en un 35%. Los halcones peregrinos concentraron su forrajeo en presas de bosques y riscos, mientras que los halcones lanarios en presas de espacios abiertos. La cercanía de parejas de congéneres obviamente no afectó los parámetros del nicho alimenticio de ninguna de las dos especies lo que sugiere que estas dos especies no estan compitiendo por comida.

[Traducción de César Márquez]

Food habits of the Peregrine Falcon (*Falco peregrinus*) have been described for arctic and temperate regions (Mearns 1983, Hunter et al. 1988, Ratcliffe 1993, Rosenfield et al. 1995), and for southwestern Australia (Pruett-Jones et al. 1981, Marchant and Higgins 1993). However, in the tropics, the diet is poorly known and data for African populations are limited (Mendelsohn 1988). The only studies of Lanner Falcon (*F. biarmicus*) diets have been in the northern periphery of its range in southern Europe, eastern Sahara, and Israel (Massa et al. 1991, Yosef 1991, Goodman and Haynes 1992). Although Peregrine Falcons share many parts of their distribution with other large falcons having similar resource needs (Cade 1982), few studies have compared Peregrine Falcon diets with those of sympatric congeners (Cade 1960, Porter and White 1973). This paper describes the diets of breeding Peregrine and Lanner Falcons in South Africa, the type and diversity of prey taken by Peregrine Falcons in different environments, defines the feeding niches of the two species in an area of sympatry and assesses the potential for competition between these two congeners in terms of diet overlap.

METHODS

We conducted our study at sites in three areas of South Africa. Sixteen pairs of Peregrine Falcons were studied on the Cape Peninsula, Western Cape Province (34°10'S, 18°25'E) from 1989–95. This area had both inland and coastal nest sites dispersed in a mosaic of urban, forest, and heathland habitats. Altitude varied from 0–1100 m and the climate was temperate with locally variable winter rainfall (400–2000 mm per year). Seven pairs of Peregrine Falcons were also monitored annually from 1989–95 on the lower Orange River, Northern Cape Province (28°30'S, 17°00'–20°40'E). This is an arid, hilly to mountainous area, sparsely vegetated except for narrow strips of riparian bush or irrigated croplands along the river banks. Altitude varied from 30–700 m and the climate was hot and dry (mean annual rainfall 60–130 mm). Prey remains were collected at seven Peregrine Falcon nest sites in the Soutpansberg range, Northern Province (23°00'S, 29°40'E) from 1988–95, and the diet of these birds was compared with that of a sympatric population of nine pairs of Lanner Falcons over a 3-yr period from 1991–93. Evergreen forest and moist woodland occurred along the eastern foot of the Soutpansberg escarpment, with dry thornveld in the west and grassland with patches of scrub forest and protea woodland along the summit of the mountains (Tarboton 1990). Altitude ranged from 900–1700 m. There was low to moderate summer rainfall (400–1000 mm per year), increasing on a gradient from

northwest to southeast, and temperatures are mild to warm.

Prey remains were collected from falcon nest ledges and from below roost sites and feeding perches. Uneaten remains, regurgitated pellets and plucked feathers were used in combination to minimize bias in diet analyses (Simmons et al. 1991, Oro and Tella 1995). Collections were made from just after egg laying to soon after fledging. The frequency of collections varied between sites, years, and areas (Table 1). Care was taken to remove all material on each collection to prevent duplication in subsequent samples. Pellets were broken up with tweezers and individual bone remnants were separated from the feather matrix.

All avian osteological material was identified using comparative skeletons in the South African Museum and additional material loaned from the Transvaal Museum, Pretoria and the National Museum, Bloemfontein. Individual body parts were separated according to taxon and recorded as the number of identified specimens (NISP). The minimum number of individuals (MNI) was calculated from the most common body part among the identified specimens, after accounting for paired elements (Klein and Cruz-Urbe 1984). Incompletely ossified bones were considered to be those of juveniles. Mammal remains were identified according to cranio-dental characteristics.

Bird and mammal remains were identified to the lowest possible taxonomic level. All prey were assigned to a size class based on bone size for unidentified prey and on body mass data from the literature (Brown et al. 1982, Smithers 1983, Maclean 1993) when prey were identified to at least the family level. Size classes were small (up to sparrow size, average about 20 g), small to medium (starling size, average about 60 g), medium (dove size, average about 130 g), medium-large (large dove size, average about 220 g), large (pigeon size and larger, average about 350 g), and very large (francolin size and larger, average about 600 g). In biomass calculations, unidentified prey were given these average mass values. Mean body mass values from the literature were used for prey identified to species. Prey identified only to higher taxonomic levels were assigned mass estimates based on published weights of similar or related forms.

Arthropod, amphibian and reptile remains were identified at a gross level only. A small number of nonavian remains were considered to be unlikely prey of falcons, particularly Peregrine Falcons, on the basis of size or habit. For example, observations suggest that African Peregrine Falcons hunt only flying prey (Hustler 1983, Tarboton 1984) and, therefore, are not likely to take terrestrial mammals and reptiles. These taxa (Appendix 1) were excluded from the analyses. Some relatively complete, easily identifiable prey were identified in the field and discarded. These were not included in the data and, to avoid duplication, only contributed to the total number of identified prey where fewer individuals of the relevant taxon were subsequently identified from other remains in the corresponding collection.

Pluckings were identified using study skins in the

Table 1. Samples of prey remains collected each year at falcon nest sites in three areas of South Africa. NISP denotes the number of identified specimens in the sample and MNI denotes the number of prey individuals identified. The MNI totals are the sum of prey individuals identified from skeletal remains, pluckings and remains identified *in situ* and discarded. Remains collected from consecutive years were pooled where sample sizes were small.

YEAR	NUMBER COLLECTIONS	NUMBER SITES	NISP	MNI			
				SKELETAL	PLUCKINGS	DISCARDED	TOTAL
Cape Peninsula Peregrine Falcons							
1989	8	1	318	37	3	22	62
1990	11	4	608	83	6	8	97
1991	7	2	187	33	8	0	41
1992	11	5	412	65	6	1	72
1993	10	5	46	63	10	1	74
1994	22	7	417	88	30	0	118
1995	7	4	161	44	4	1	49
Overall	76	10	2649	413	67	33	513
Orange River Peregrine Falcons							
1989–90	7	5	680	102	10	0	112
1991–92	4	4	410	72	8	1	81
1993–95	4	2	333	48	7	0	55
Overall	15	7	1423	222	25	1	248
Soutpansberg Peregrine Falcons							
1988–90	5	4	245	36	6	4	46
1991	13	6	719	113	8	0	121
1992	13	5	378	89	5	0	94
1993	14	4	585	93	10	0	103
1994–95	4	3	225	41	2	0	43
Overall	49	7	2152	372	31	4	407
Soutpansberg Lanner Falcons							
1991	14	9	178	65	5	0	70
1992	15	7	302	62	3	0	65
1993	10	7	188	38	0	1	39
Overall	39	9	668	165	8	1	174

South African Museum. No attempt was made to determine the number of individuals represented by the sum of pluckings of a particular species collected in each sample. To prevent duplication in these samples, species identified from feather remains contributed one individual to the total for a collection, but only when the relevant taxon was not recorded in the skeletal remains. Juveniles were identified from plumage characteristics where these differed from adult birds, and from the predominance of sheathed or incompletely grown tail or flight feathers, which indicated that nestling or recently fledged individuals had been taken.

Some dietary data were obtained from field observations. These were used to determine bias in the analyses of prey remains (Collopy 1983, Rosenberg and Cooper 1990). Nearly 1000 hr of observations were made at Peregrine Falcon nest sites on the Cape Peninsula, and over 200 hr were obtained each at nest sites on the Orange River and in the Soutpansberg and at Lanner Falcon sites in the Soutpansberg. Observations were made using 10

× 40 binoculars or a 20–60× spotting scope from distances of 200–400 m. Whenever a falcon was seen with food, an effort was made to identify or at least estimate the size of its prey. Size classes used were the same as those used for prey remains. Only largely intact prey could be identified or size classified.

Indices of diet breadth and overlap were calculated based on the relative frequency of taxa identified in prey remains at the species level wherever possible to refine the quality of these estimates (Greene and Jaksic 1983, Sherry 1990). Diet breadth (B_A) was calculated using Levins' (1968) standardized formula:

$$B_A = B - 1/n - 1,$$

where $B = 1/\sum p_i^2$ and p_i is the proportion of the diet contributed by the i th taxon. Values of B_A range from 0–1, with larger values indicating a broader diet. Also, the number of frequently used taxa (those comprising 3% or more of the total number of identified prey; Krebs 1989) was tallied for each falcon population as an additional

estimate of diet breadth. Diet overlap was measured using Morisita's (1959) index of similarity:

$$C = 2 \sum p_{ij}p_{ik} / \sum p_{ij} \left[\frac{(n_{ij} - 1)}{(N_j - 1)} \right] + \sum p_{ik} \left[\frac{(n_{ik} - 1)}{(N_k - 1)} \right]$$

where p_i and p_{ik} are the proportions that taxon i makes up of the diets of species j and k , respectively, n_{ij} and n_{ik} are the number of individuals of taxon i in the diets of species j and k , respectively, and N_j and N_k are the total number of individuals in the diets of species j and k , respectively. Values of C range from 0–1, with larger values indicating a greater dietary overlap. This index is considered the least prone to biases associated with sample size and the number of resources used (Smith and Zaret 1982). Multivariate cluster analyses were conducted to examine qualitative differences in the diet of sympatric Peregrine and Lanner Falcons, using the PRIMER software package (Plymouth Marine Laboratory, U.K.). Diet composition data were compared using the Bray-Curtis similarity coefficient (using group average linking) to generate a dendrogram of hierarchical clusters and a process of nonmetric multidimensional scaling to generate an ordination plot.

To examine the possible competitive influence of nearby Lanner Falcon pairs on the diet of Soutpansberg Peregrine Falcons and *vice versa*, the food niche parameters of falcon pairs with congeners as particularly close neighbors (pairs <1 km apart, Peregrine Falcons $N = 3$, average distance to nearest Lanner Falcon pair = 0.6 km, Lanner Falcons $N = 4$, average distance to nearest Peregrine Falcon pair = 0.7 km) were compared with those of relatively isolated pairs (>2 km apart, Peregrine Falcons $N = 4$, average distance to nearest Lanner Falcon pair = 6.5 km, Lanner Falcons $N = 5$, average distance to nearest Peregrine Falcon pair = 4.7 km). The mean distance between conspecific pairs was 9.7 km for Peregrine and 5.2 km for Lanner Falcons.

Two sampling techniques were used to estimate the abundance and distribution of potential avian prey in the vicinity of falcon nest sites in an attempt to make qualitative assessments of prey selection and habitat use. An estimate of local prey availability was made at nest cliffs by counting the number of potential prey per hour which flew across a sampling area prescribed by a 1 m² frame. This frame was positioned at the top of the cliff, looking out and down, or on the scree slope below the face looking up at the crest. An observer sat 2 m behind the frame, looking through it, to make the count. Prey counts were made at different times of the day at a cross-section of nest sites on the Cape Peninsula and in the Soutpansberg only, mostly from 1991–93.

Line-transect counts were walked in the Soutpansberg to estimate bird densities in seven habitats identified in terms of a broad-scale classification of the character and structure of vegetation present (*sensu* Edwards 1983). Plains to the south of the mountain range comprised either short, semi-open savanna woodland or short, sparse denuded woodland, often found adjacent to rural settlements and heavily impacted by clearing and cultivation. Forest and plantation included tall, closed stands of both indigenous evergreen and exotic eucalyptus or pine forest. Areas of montane grassland and scrub forest were typical of the upper slopes of the mountains and featured

low, open grassland with patches of short deciduous forest. Deciduous woodland comprised short, moderately closed woodland and occurred on the northern backslopes and on the middle and upper slopes at the western end of the range. The lower scree slopes of the escarpment were thickly vegetated with low, closed woodland or moist thornscrub in the east and short, moderately closed woodland or dry thornscrub further west. One or two sites were selected as typical of each habitat type and at least three 1 km line transects were walked at these sites each breeding season from 1991–93. Transect sites were located between 150–3000 m from the main escarpment. Transects were completed at various times of day, but mostly in the morning or in late afternoon. Transects were walked briskly so only the birds which were conspicuously active in the area, and hence most likely to provide falcons with hunting opportunities, were recorded. High, overflying birds unlikely to be resident in the habitat being sampled were not counted, and species considered too large for falcons to catch and subdue under normal circumstances (>800 g in weight) were also excluded. The species, number of individuals and approximate perpendicular distance from the transect line were recorded for each sighting (Bibby et al. 1992).

RESULTS

A minimum of 1168 individuals of at least 82 species from 34 families were identified as prey from the remains collected at Peregrine Falcon nest sites, and a minimum of 174 individuals of at least 24 species from 15 families were identified from Lanner Falcon prey remains (Table 1, Appendix 1). Samples of remains collected at Peregrine Falcon sites in the Soutpansberg were more substantial than those from sympatric Lanner Falcon sites, yielding more specimens per collection (Peregrine Falcon $\bar{x} = 45.6$, range = 2–211, $N = 47$ collections; Lanner Falcon $\bar{x} = 18.6$, range = 1–60, $N = 36$ collections; Mann-Whitney $Z = 3.01$, $P = 0.003$) and more identified individuals per collection (Peregrine Falcon $\bar{x} = 8.0$, range = 1–31, $N = 49$ collections; Lanner Falcon $\bar{x} = 4.5$, range = 1–10, $N = 39$ collections; $Z = 2.77$, $P = 0.006$).

Peregrine Falcons were observed catching or feeding on 296 prey individuals, about half of which could be identified at least to family. Fifteen species from eight families were identified. Only one species, Black-eyed Bulbul (*Pycnonotus barbatulus*) was observed as Peregrine Falcon prey and not recorded in prey remains. Only 36 prey individuals were identified during observations at Lanner Falcon sites in the Soutpansberg. These comprised one locust, one 1–3 day-old chicken (*Gallus gallus*), one *Streptopelia* dove, one unidentified murid rodent, seven unidentified small birds, nine small-

medium birds, 12 medium birds, and four medium-large birds.

Because relatively few prey items were identified in the field, and the sample of observed prey at Lanner Falcon sites was so small, the quality of the diet information provided by the analysis of prey remains could only properly be assessed in terms of the size of prey observed at Peregrine Falcon sites in each area. These comparisons suggested that remains collected on the Cape Peninsula provided the least accurate diet estimate, while those from sites in the Soutpansberg were the most accurate (Fig. 1). On average, prey remains underrepresented smaller prey by about 10% and overrepresented larger prey by about 8%. Taxonomically the samples were similar with birds, and particularly columbids, predominating in all.

The relative importance of key species in the diets of both falcons was fairly consistent between years, so data on prey remains for each year were pooled. Dominant species in the diet of Peregrine Falcons on the Cape Peninsula were Laughing Dove (*Streptopelia senegalensis*, 28% by frequency and 20% by biomass), European Starling (*Sturnus vulgaris*, 14 and 7%, respectively), and Cape Turtle Dove (*Streptopelia capicola*). Peregrine Falcons on the Orange River took Rock Pigeons (*Columba guinea*, 15 and 41%, respectively), Namaqua Sandgrouse (*Pterocles namaqua*, 10 and 13%, respectively), and Laughing Dove (8 and 6%, respectively). Peregrine Falcons in the Soutpansberg took Laughing Doves (19 and 16%, respectively), Red-faced Mousebirds (*Urocolius indicus*, 10 and 4%, respectively), and Red-eyed Doves (*Streptopelia semitorquata*, 8 and 16%, respectively). During 1991–93, Peregrine Falcons in the Soutpansberg preyed mainly on doves (35 and 45%, respectively) and mousebirds (15 and 7%, respectively), while sympatric Lanner Falcons took chickens (40 and 30%, respectively), doves (20 and 25%, respectively), and Crowned Plovers (*Vanellus coronatus*, 9 and 12%, respectively; Appendix 1).

The relative importance of juvenile birds in the diets of Peregrine Falcons varied significantly ($\chi^2 = 19.5$, $P < 0.001$) among the three study areas. Most of the juveniles recorded were columbids (Appendix 1) and juveniles were more frequent in the diet on the Cape Peninsula (32 of 513 individuals or 6.2%) than in the Soutpansberg (3 of 407 or 0.7%; χ^2_1 with Yates' correction = 15.3, $P < 0.001$), and comprised 3.2% of the diet of Pere-

grine Falcons on the Orange River. The relative frequency of juveniles in the diet of Cape Peninsula Peregrine Falcons increased through the breeding season from 1.7% by frequency in late October to 6.2% in early November, 6.8% in late November, and 8.1% in early December. A high proportion of the remains recovered from Lanner Falcon nests were young chickens, and juvenile birds comprised 39.7% of identified prey from these sites.

Columbids made up the majority of prey taken by Peregrine Falcons in all three study areas (Table 2). Other consistently important taxa were species in the families Apodidae, Sturnidae and Ploceidae. Soutpansberg Lanner Falcons took mainly phasianids, charadriids and columbids. The average size of prey taken by Peregrine Falcons in each of the three study areas varied (Kruskal-Wallis $H = 26.8$, $P < 0.001$). Cape Peninsula Peregrine Falcons took significantly larger prey (average mass = 144.5 g, range = 15–390 g, $N = 513$ individuals) than Orange River Peregrine Falcons (average mass = 128.3 g, range = 3–347 g, $N = 248$ individuals; Mann-Whitney $Z = 4.33$, $P < 0.001$) and Peregrine Falcons in the Soutpansberg (average mass = 123.3 g, range = 3–600 g, $N = 407$ individuals; $Z = 4.11$, $P < 0.001$). On average, Soutpansberg Peregrine Falcons took significantly smaller prey (average mass = 116.9 g, range = 3–600 g, $N = 318$ individuals) than sympatric Lanner Falcons (average mass = 123.7 g, range = 3–500 g, $N = 174$ individuals; $Z = 2.41$, $P = 0.02$). Peregrine Falcon diet included a greater proportion of small and large prey individuals, while Lanner Falcons tended to concentrate on medium-sized prey.

Of the three Peregrine populations studied, those on the Cape Peninsula had the least diverse diet (30 species were identified from prey remains; Appendix 1) and the narrowest diet breadth ($B_A = 0.17$). Peregrine Falcons in the Soutpansberg fed on a wide diversity of prey (≥ 50 species) but concentrated on a few taxa and had a moderate diet breadth ($B_A = 0.21$). On the Orange River, only 38 species were taken but there was less emphasis on particular families so the diet was relatively broad-based ($B_A = 0.34$).

Overall, Peregrine Falcons in the Soutpansberg had a broader feeding niche than sympatric Lanner Falcons and there was some overlap in the diets of the two species ($C = 0.34$). On a per site basis (excluding one peregrine site and one lanner site with insufficient samples), the difference in

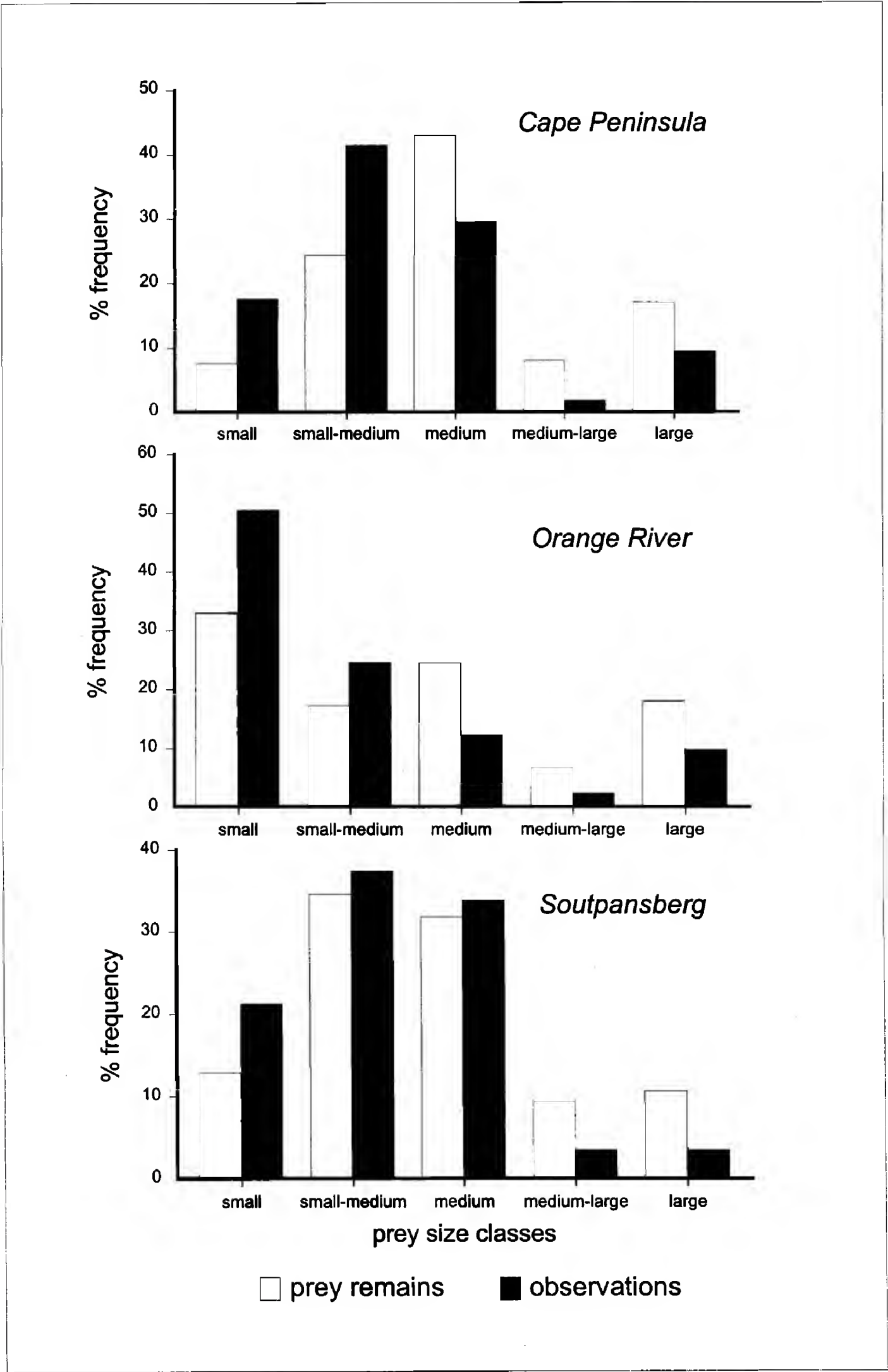


Figure 1. The relative frequency of prey of different size classes in the diets of Peregrine Falcons in three areas of South Africa determined from the analysis of prey remains and direct observations. Prey remains differed significantly from observations on the Cape Peninsula (remains $N = 513$, observations $N = 159$, $\chi^2_4 = 42.0$, $P < 0.001$) and on the Orange River (remains $N = 248$, observations $N = 81$, $\chi^2_4 = 14.0$, $P = 0.007$) but not in the Soutpansberg (remains $N = 407$, observations $N = 56$, $\chi^2_4 = 7.3$, $P = 0.12$).

Table 2. Summary of falcon diets from the analysis of prey remains collected at nest sites (see Appendix 1 for raw data). The importance of each taxon is expressed in terms of its relative frequency in the sample of individuals (%F) and in terms of its contribution to the total biomass of prey in each sample (%M). Families comprising 1% or more of the diet in each sample are listed. Peregrine Falcons (all years): Cape Peninsula $N = 513$ individuals, 74 107 g; Orange River $N = 248$ individuals, 31 811 g; and Soutpansberg $N = 407$ individuals, 50 193 g. Soutpansberg (1991–93): Peregrine Falcons $N = 318$ individuals, 37 188 g; Lanner Falcons $N = 174$ individuals, 21 532 g.

FAMILY	PEREGRINE FALCONS (1989–95)						SOUTPANSBERG (1991–93)			
	CAPE PENINSULA		ORANGE RIVER		SOUTPANSBERG		PEREGRINES		LANNERS	
	%F	%M	%F	%M	%F	%M	%F	%M	%F	%M
Phasianidae	—	—	—	—	1.5	3.6	1.3	3.6	40.2	37.4
Charadriidae	1.0	—	—	—	3.9	5.3	3.5	4.9	9.2	12.4
Recurvirostridae	—	—	—	—	—	—	—	—	1.2	1.6
Glareolidae	—	—	—	—	1.0	—	—	—	—	—
Laridae	—	—	2.4	2.1	—	—	—	—	—	—
Pteroclididae	—	—	9.7	14.0	1.0	1.9	—	1.3	—	—
Columbidae	66.1	85.1	37.5	69.9	48.2	68.4	46.5	67.2	28.2	39.1
Psittacidae	1.0	—	—	—	—	—	—	—	—	—
Apodidae	6.2	1.9	10.1	4.1	6.1	2.9	5.4	2.7	1.2	—
Coliidae	1.0	—	1.2	—	13.5	6.1	14.8	7.0	—	—
Alaudidae	—	—	7.7	1.0	1.0	—	1.3	—	—	—
Hirundinidae	—	—	6.1	—	—	—	—	—	—	—
Sturnidae	15.0	8.2	1.6	1.4	3.2	2.3	3.1	2.1	—	—
Ploceidae	4.5	1.1	4.4	—	4.2	1.0	4.4	1.2	4.6	1.2
Estrildidae	—	—	1.2	—	—	—	—	—	—	—
Fringillidae	—	—	1.6	—	1.0	—	—	—	1.2	—
Molossidae	—	—	6.5	—	—	—	—	—	—	—
Pteropodidae	—	—	—	—	1.5	1.6	1.3	1.4	—	—
Muridae	—	—	—	—	—	—	—	—	1.2	—

diet breadth was statistically significant (Peregrine Falcon average $B_A = 0.14$, range = 0.11–0.18, $N = 6$; Lanner Falcon average $B_A = 0.04$, range = 0.01–0.14, $N = 8$; Mann-Whitney $Z = 2.52$, $P = 0.01$). Cluster analyses on diet composition data clearly separated Peregrine and Lanner Falcon sites (Fig. 2). Food-niche widths of falcon pairs with pairs of congeners as close neighbors did not differ significantly from those of more isolated pairs (Peregrine Falcon pairs with close neighboring Lanner Falcon pairs average $B_A = 0.14$, $N = 3$, isolated pairs average $B_A = 0.14$, $N = 3$, $Z = 1.00$, $P = 1.00$; Lanner Falcon pairs with close neighboring Peregrine Falcon pairs average $B_A = 0.08$, $N = 4$, isolated pairs average $B_A = 0.05$, $N = 4$, $Z = 0.72$, $P = 0.47$). However, collectively, interspecific diet overlap was greatest between pairs with close neighboring congeners (close pairs $C = 0.44$, distant pairs $C = 0.26$).

Counts at cliffs on the Cape Peninsula and in the Soutpansberg had similar average prey passage

rates in terms of numbers of individuals counted (Cape Peninsula average = 116.3 birds per hour, range = 2–542 birds per hour, $N = 64$ counts; Soutpansberg average = 119.0 birds per hour, range = 0–929 birds per hour, $N = 114$ counts). A significantly greater biomass of birds per hour was recorded in counts on the Cape Peninsula (average = 8567 g per hour, range = 405–33 479 g per hour, $N = 64$ counts) than in the Soutpansberg (average = 7104 g per hour, range = 0–56 669 g per hour, $N = 114$ counts; Mann-Whitney $Z = 3.09$, $P = 0.002$). Mostly cliff-dwelling species were included in these counts (e.g., Rock Pigeons, Alpine Swifts [*Apus melba*] and Red-winged Starlings [*Onychognathus morio*]). Larger species were more abundant at cliffs on the Cape Peninsula than in the Soutpansberg (e.g., Rock Pigeons were recorded in 72 vs. 18% of counts at cliffs on the Cape Peninsula and in Soutpansberg, respectively, with an average of 3.9 vs. 0.6 individuals per count), whereas aerial insectivores were more abundant in

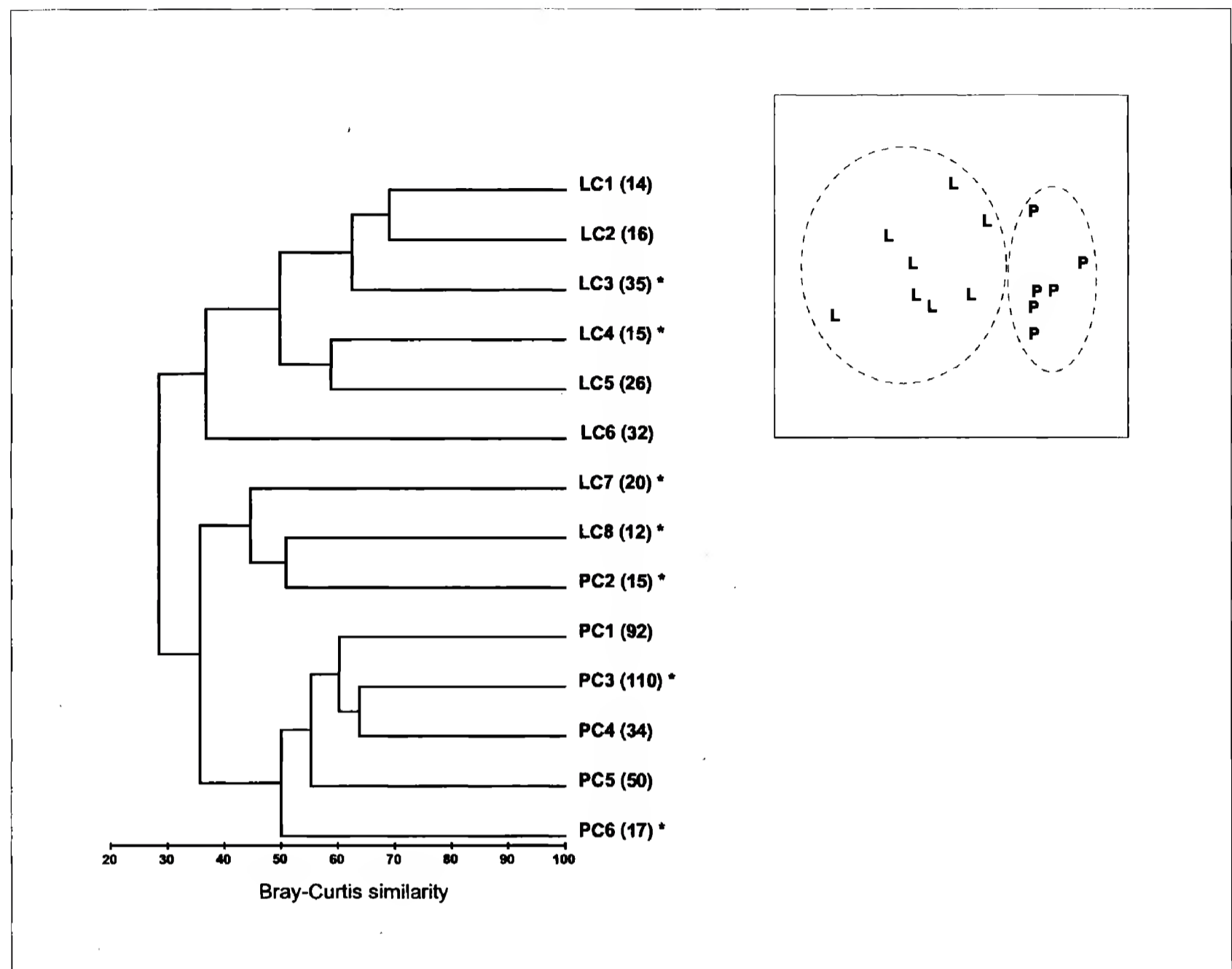


Figure 2. Results of cluster analyses on diet composition data for Peregrine (P) and Lanner (L) Falcon sites in the Soutpansberg. The dendrogram groups sites according to the Bray-Curtis similarity coefficient (with the number of prey individuals identified from each site in parentheses). Sites with close neighboring pairs of congeners are marked with an asterisk. The ordination plot (inset) illustrates the relatedness of each site to the others in terms of a multidimensional scaling procedure.

the Soutpansberg (e.g., Rock Martins [*Hirundo fuligula*] were recorded in 19 vs. 52%, respectively, with an average of 0.8 vs. 10.2 individuals per count).

Of the habitats identified in the Soutpansberg, the woodlands on the plain below the escarpment supported the highest diversity and the greatest number and biomass of birds (average = 6–7 species, 20–30 individuals and 800–1300 g per transect, respectively), while the dense thornscrub on the scree slopes of the mountains featured the most depauperate avifauna (average = <2 species, 2–6 individuals and 40–200 g per transect). Transect data extrapolated to avian density estimates ranging from 1441–1690 individuals/km² in savan-

na and denuded woodland to only 189 individuals/km² in moist thornscrub.

Some species which were recorded regularly in the diet of falcons in the Soutpansberg were not common in the environment. In particular, Red-faced Mousebirds made up about 10% of the Peregrine Falcon diet by frequency but were not encountered on any of the transect counts. Three species (Chestnut-backed Finchlark [*Eremopterix leucotis*], Melba Finch [*Pytilia melba*] and Blue Waxbill [*Uraeginthus angolensis*]) were common on the plains at the foot of the escarpment (\bar{x} = 13.6, 1.5, and 8.5 individuals, respectively, of each species were recorded per transect through savanna or denuded woodland) but were infrequent or did not

Table 3. Foraging habitat use by breeding Peregrine and Lanner Falcons in the Soutpansberg as inferred from the habitat affinities of prey species identified in food remains. (A) only indicates prey species which were recorded in passage-rate or line-transect counts. (B) combines the species in (A) with a number of important prey species which were not sighted on sample counts (e.g., domestic chicken, Namaqua Dove and Red-faced Mousebird). Habitat preferences in species in (A) were determined from count data. The additional species in (B) were assigned to habitats on the basis of incidental observations in the area. Both comparative distributions were significantly different: (A) $\chi^2_6 = 12.6$, $P = 0.049$; (B) $\chi^2_6 = 79.7$, $P < 0.001$.

FAVORED HABITAT OF PREY SPECIES	% FREQUENCY IN PEREGRINE DIET		% FREQUENCY IN LANNER DIET	
	(A)	(B)	(A)	(B)
Savanna woodland	26.7	39.0	19.0	19.5
Denuded woodland	7.9	12.3	12.1	49.4
Forest and plantation	0.3	0.3	—	—
Grassland and scrub forest	5.4	5.4	1.4	1.4
Moist thornscrub	—	—	—	—
Deciduous woodland	0.3	0.3	1.4	1.4
Dry thornscrub	0.3	0.3	—	—
Cliffs	9.1	9.1	5.2	5.2

occur in falcon diets, perhaps because these small birds were underrepresented in prey remains. Similarly, Black-eyed Bulbuls were ubiquitous in the area (0.5–1.6 individuals per transect in all habitats except denuded woodland), but were recorded as falcon prey only once. There was a significant difference in the foraging habitats used by Peregrine and Lanner Falcons in the Soutpansberg, as inferred from the habitat preferences of their prey (Table 3). While both species favored the wooded plains below the mountain range, Peregrine Falcons took more woodland species from relatively pristine habitats whereas Lanner Falcons took open-country species from denuded woodland and free-range chickens from around human settlements. Also, Peregrine Falcons preyed more heavily than Lanner Falcons on cliff-dwelling species (Table 3). Soutpansberg Peregrine Falcons took significantly more ‘commuter species’ (aerial insectivores, migrants or species which regularly commute between distant resources, e.g., sandgrouse, large columbids) than sympatric Lanner Falcons (76 of 318 or 23.9% vs. 19 of 174 or 10.9% commuters, respectively; $\chi^2_1 = 11.3$, $P < 0.001$), but fewer overall than Cape Peninsula Peregrine Falcons (27.0 vs. 31.6% commuters, respectively) and significantly fewer than Peregrine Falcons on the Orange River (110 of 407 or 27.0% vs. 114 of 248 or 46.0% commuters, respectively; $\chi^2_1 = 23.7$, $P < 0.001$).

DISCUSSION

Columbids and particularly *Streptopelia* doves appear to be the staple food of Peregrine Falcons in southern Africa (Hustler 1983, Tarboton 1984, Mendelsohn 1988, this study). A similar preference for columbiforms has been recorded in many other areas of the Peregrine Falcon’s distribution where pigeons and doves are available prey (Cade 1982, Ratcliffe 1993). Small, aerially dexterous species such as swifts and bats appear more consistently in the diet of African Peregrine Falcons than has generally been reported for other populations (Hustler 1983, Brown 1988, Mendelsohn 1988). Conversely, relatively large, terrestrial species such as anatids, galliforms, and charadriiforms are less frequently taken in Africa than in other areas (Cade 1960, Porter and White 1973, Pruett-Jones et al. 1981, Mearns 1983, Ratcliffe 1993). These differences may partly reflect differences in prey availability, but may also be due to a greater tendency for African Peregrine Falcons (and perhaps other small, tropical forms of the species) to ‘catch and carry’ prey rather than strike it to the ground and retrieve it (Cade 1982).

Three *Streptopelia* doves comprised nearly half (by frequency and mass) of the diet of Peregrine Falcons on the Cape Peninsula. British Peregrine Falcons specialize to a similar degree on larger columbids (Mearns 1983, Ratcliffe 1993). Typical of peri-urban peregrine populations around the

world (Cade and Bird 1990), Cape Peninsula pairs also took substantial numbers of commuting feral or domestic pigeons (*Columba livia*) and European Starlings, and occasionally preyed on escaped aviary birds. Inexperienced, newly-fledged birds are particularly vulnerable to predation by raptors (Newton and Marquiss 1982, Rosenfield et al. 1995), and young doves and starlings were taken quite frequently by Cape Peninsula Peregrine Falcons. As observed in other temperate falcon populations (Newton et al. 1984, Parr 1985), juvenile birds became more prevalent in the diet as the breeding cycle progressed. This supports the contention that breeding by Peregrine Falcons on the Cape Peninsula may in part be timed to exploit the period of maximum productivity of their principal prey species (Jenkins 1991, 1998).

Streptopelia doves featured least prominently in the diet of Peregrine Falcons on the Orange River, the most generalized feeders of the three Peregrine Falcon populations studied. These falcons usually foraged in the river valley (Jenkins 1995), which was the focus of bird movements in the area. Aerial insectivores (swifts, hirundines, and microchiropteran bats) and obligate drinkers (sandgrouse, columbids, and granivorous passerines) were the groups most frequently taken and were probably exposed to attack crossing rocky gorges or open stretches of the river, or traveling over arid flats adjacent to the floodplain.

Soutpansberg Peregrine Falcons preyed on a wide variety of species, most of which were secured in bird-rich woodlands at least 2 km from the base of the escarpment. Relatively fewer transient or commuter species, and more sedentary residents, were taken by these pairs than by Peregrine Falcons in the other two areas. However, the woodland species recorded as prey were generally those likely to fly furthest from, and highest above, the protective canopy of trees (e.g., Red-faced Mousebirds, *Lamprolornis* starlings). Mousebirds were more common Peregrine Falcon prey in the Soutpansberg than has been found in studies at other woodland sites, whereas rollers and woodpeckers were not taken (Hustler 1983, Tarboton 1984), perhaps because they were less common in the environment. Francolins are among the largest species regularly taken by African Peregrine Falcons, and those recorded as prey of Soutpansberg Peregrine Falcons were probably all caught by females. These essentially cursorial birds may have been caught in flight as they descended from the top of

the cliff-line to the scree slopes below, as suggested by Hustler (1983).

Diet breadth indices calculated for South African Peregrine Falcons are comparable with equivalent data for populations in other areas (Table 4). These figures suggest that peregrines in temperate areas (e.g., the Cape Peninsula [this study], southern Scotland [Mearns 1983], Victoria, Australia [Pruett-Jones et al. 1981]) are relatively specialized feeders. In contrast, Peregrine Falcons appear to become more generalized in extreme environments such as deserts (e.g., this study), taiga and tundra (Cade 1960, Cade et al. 1968).

Relatively small samples of identifiable prey remains were recovered from Lanner Falcon nest sites, perhaps because much of the prey they consumed was completely digestible. Few data are available on the diet of southern African Lanner Falcons. The only quantitative studies, based on small samples, suggest that phasianids (including domestic fowl) and columbids are important prey groups (Barbour 1971, Tarboton and Allan 1984, Kemp 1993). Lanner Falcons in the Soutpansberg were relatively specialized feeders, with young chickens comprising nearly 40% of the prey recorded in remains. Given the greater susceptibility of juvenile bones to damage and acid erosion, chickens may have been underrepresented in these samples. Columbids were also important, and contributed more than phasianids to the biomass of identified prey. Sources of free-ranging poultry were a considerable distance from most Lanner Falcon nest sites, and their frequency in prey remains suggests that Lanner Falcon hunting ranges extended well beyond those of nearby Peregrine Falcon pairs. One radio-tracked male Lanner Falcon foraged over rural settlement areas >10 km from the main escarpment. Terrestrial or cursorial species predominated in the diet of Soutpansberg Lanner Falcons, and most prey were probably taken on or close to the ground.

Southern African Peregrine and Lanner Falcons are of approximately equal body mass and comparisons of key food handling and flight performance measurements yield ratios consistently lower than values traditionally considered minimum for noncompetitive coexistence (Jenkins 1998). Despite these structural similarities, diet overlap between Soutpansberg Peregrine and Lanner Falcons was moderate relative to those calculated using data from other studies of Peregrine Falcons and sympatric congeners, and fell well below the

Table 4. Indices of Peregrine Falcon diet breadth for a number of locations around the world, and measures of diet overlap between Peregrine Falcons and sympatric congeners.

STUDY POPULATION	NUMBER OF TAXA USED	NUMBER OF TAXA >3%	DIET BREADTH (B_A)
Southern Scotland ¹	90	5	0.04
Victoria, Australia ²	77	6	0.12
Cape Peninsula, South Africa ³	39	6	0.17
Soutpansberg, South Africa ⁴	63	9	0.21
West Greenland ⁵	11	6	0.24
NW Territories, Canada ⁶	19	7	0.34
Orange River, South Africa ⁷	45	10	0.34
Taiga zone, Alaska ⁸	61	11	0.81
Sympatric Peregrine Falcons and Gyrfalcons (<i>F. rusticolus</i>), Colville River, Alaska ⁹			
Peregrine Falcon	55	12	0.33
Gyrfalcon	55	2	0.004
Diet overlap: $C = 0.07$			
Sympatric Peregrine and Lanner Falcons, Soutpansberg, South Africa ¹⁰			
Peregrine Falcon	67	10	0.20
Lanner Falcon	67	6	0.07
Diet overlap: $C = 0.34$			
Sympatric Peregrine and Prairie Falcons (<i>F. mexicanus</i>), Wasatch Mountains, Utah ¹¹			
Peregrine Falcon	33	9	0.31
Prairie Falcon	33	6	0.26
Diet overlap: $C = 0.58$			

Food niche parameters were calculated using data from: ¹ Mearns 1983, ² Pruett-Jones et al. 1981, ³ this study, ⁴ this study (all years), ⁵ Rosenfield et al. 1995, ⁶ Bradley and Oliphant 1991, ⁷ this study, ⁸ Cade et al. 1968, ⁹ Cade and White 1971, ¹⁰ this study (1991–93), ¹¹ Porter and White 1973.

suggested critical value for competing species of about 0.62 (Bosakowski and Smith 1992). Also, while competition theory predicts narrower food niches and reduced diet overlap between close pairs of competing species vs. distant pairs (Nilsson 1984, Korpimäki 1987), the diet of falcon pairs in this study was not obviously affected by the presence of nearby pairs of congeners. Therefore, there was little evidence suggesting active competition for food between Peregrine and Lanner Falcons in the Soutpansberg. As concluded in previous studies of Peregrine Falcons and sympatric congeners (e.g., Cade 1960, Porter and White 1973), relatively subtle differences in morphology, flying performance, and hunting techniques (Jenkins 1995) are evidently sufficient to segregate foraging habitat and diet of Peregrine and Lanner Falcons in South Africa.

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Appendix 1. Invertebrate and vertebrate taxa identified from remains collected at Peregrine and Lanner Falcon nest sites in South Africa. Remains were collected at 10 Peregrine Falcon sites on the Cape Peninsula, seven Peregrine Falcon sites on the Orange River, and seven Peregrine Falcon sites and nine Lanner Falcon sites in the Soutpansberg. Data provided are the average mass of each taxon and the number of individuals identified, with the number of nest sites at which each taxon was collected in parentheses. Items marked with an asterisk were not considered as falcon prey in the diet analyses.

PREY TAXON	AVERAGE MASS (g)	CAPE PENINSULA	ORANGE RIVER	SOUTPANSBERG	
				PEREGRINES	LANNERS
Insects					
Unidentified orthopterans	3	—	1 (1)	12 (2)	3 (2)
Unidentified coleopterans	3	—	1 (1)	2 (1)	—
Amphibians					
Unidentified frogs	20	—	—	*2 (1)	—
Birds					
Little Sparrowhawk—male	80	—	—	1 (1)	—
<i>Accipiter minullus</i>					
Peregrine Falcon—nestling	250	—	—	*2 (2)	—
Lanner Falcon—nestling	250	—	—	—	*1 (1)
Coqui Francolin	230	—	—	1 (1)	—
<i>Francolinus coqui</i>					
Crested Francolin	340	—	—	2 (1)	1 (1)
<i>F. sephaena</i>					
Grey-wing Francolin	390	1 (1)	—	—	—
<i>F. africanus</i>					
Cape Francolin—pullus	150	—	1 (1)	—	—
<i>F. capensis</i>					
Natal Francolin—female	425	—	—	2 (2)	—
<i>F. natalensis</i>					
Natal Francolin—unsexed	520	—	—	—	1 (1)
Unidentified adult francolin	500	—	—	—	2 (2)
Unidentified pullus francolin	150	—	—	—	1 (1)
Domestic chicken—<3days old	60	—	—	—	41 (8)
<i>Gallus gallus</i>					
Domestic chicken—±7 days old					
Domestic chicken—±14 days old	150	—	—	—	23 (3)
Harlequin Quail	250	—	—	—	1 (1)
<i>C. delegorguei</i>					
White-fronted Plover					
<i>Charadrius marginatus</i>	49	2 (2)	—	—	—
Kittlitz Plover					
<i>C. pecuarius</i>	43	2 (1)	—	—	—

Appendix 1. Continued.

PREY TAXON	AVERAGE MASS (g)	CAPE PENINSULA	ORANGE RIVER	SOUTPANSBERG	
				PEREGRINES	LANNERS
Crowned Plover—adult	167	1 (1)	—	16 (5)	14 (6)
<i>Vanellus coronatus</i>					
Crowned Plover—immature	167	—	—	—	2 (2)
Greenshank	191	—	1 (1)	—	1 (1)
<i>Tringa nebularia</i>					
Curlew Sandpiper	57	3 (1)	—	—	—
<i>Calidris ferruginea</i>					
Little Stint	24	—	1 (1)	—	—
<i>C. minuta</i>					
Black-winged Stilt	175	—	—	2 (1)	2 (2)
<i>Himantopus himantopus</i>					
Temminck's Courser	74	—	—	4 (3)	—
<i>Cursorius temminckii</i>					
Common Tern	124	2 (1)	3 (1)	—	—
<i>Sterna hirundo</i>					
White-winged Tern	57	—	1 (1)	—	—
<i>Chlidonias leucopterus</i>					
Unidentified Tern	100	—	2 (2)	—	—
Namaqua Sandgrouse	185	—	24 (6)	—	—
<i>Pterocles namaqua</i>					
Burchell's Sandgrouse	235	—	—	1 (1)	—
<i>P. burchelli</i>					
Double-banded Sandgrouse	235	—	—	3 (2)	—
<i>P. bicinctus</i>					
Feral or domestic pigeon—adult	320	47 (7)	8 (4)	17 (3)	—
<i>Columba livia</i>					
Feral or domestic pigeon—young	320	1 (1)	—	—	—
Rock Pigeon—adult	347	28 (7)	35 (6)	20 (5)	6 (2)
<i>C. guinea</i>					
Rock Pigeon—fledgling	347	8 (3)	2 (2)	1 (1)	1 (1)
Rameron Pigeon	415	—	—	2 (2)	—
<i>C. arquatrix</i>					
Unidentified pigeon—adult	330	1 (1)	—	—	—
Unidentified pigeon—young	330	2 (2)	—	—	—
Red-eyed Dove—adult	235	40 (7)	16 (5)	34 (6)	10 (4)
<i>Streptopelia semitorquata</i>					
Red-eyed Dove—fledgling	235	1 (1)	—	—	—
Cape Turtle Dove	153	61 (7)	5 (4)	25 (5)	8 (5)
<i>S. capicola</i>					
Laughing Dove—adult	102	140 (8)	20 (5)	79 (7)	21 (7)
<i>S. senegalensis</i>					
Laughing Dove—fledgling	102	4 (2)	—	—	2 (2)
Unidentified dove—fledgling	130	3 (3)	—	—	—
Namaqua Dove	40	3 (3)	7 (5)	15 (5)	—
<i>Oena capensis</i>					
Green-spotted Dove	65	—	—	1 (1)	1 (1)
<i>Turtur chalcospilos</i>					
Small unidentified columbid	50	—	—	1 (1)	—
Medium unidentified columbid	160	—	—	1 (1)	—
Cockatiel	90	1 (1)	—	—	—
<i>Nymphicus hollandicus</i>					

Appendix 1. Continued.

PREY TAXON	AVERAGE MASS (g)	CAPE PENINSULA	ORANGE RIVER	SOUTPANSBERG	
				PEREGRINES	LANNERS
Budgerigar	28	4 (1)	—	1 (1)	—
<i>Melopsittacus undulatus</i>					
Grey Loerie	269	—	—	1 (1)	—
<i>Corythaixoides concolor</i>					
Freckled Nightjar	60	—	2 (1)	—	—
<i>Caprimulgus tristigma</i>					
Unidentified nightjar	60	—	—	1 (1)	—
Black Swift—adult	45	13 (5)	—	12 (3)	—
<i>Apus barbatus</i>					
Black Swift—fledgling	45	1 (1)	—	—	—
Bradfield's Swift	45	—	18 (6)	—	—
<i>A. bradfieldi</i>					
Little Swift	26	12 (3)	—	2 (2)	—
<i>A. affinis</i>					
Alpine Swift	77	6 (4)	6 (5)	11 (3)	2 (2)
<i>A. melba</i>					
Unidentified swift	35	—	1 (1)	—	—
Speckled Mousebird	53	—	—	14 (6)	1 (1)
<i>Colius striatus</i>					
White-backed Mousebird—adult	41	1 (1)	2 (2)	—	—
<i>C. colius</i>					
White-backed Mousebird—fledgling	41	—	1 (1)	—	—
Red-faced Mousebird	56	4 (3)	—	41 (7)	—
<i>Urocolius indicus</i>					
Narina Trogon	65	—	—	1 (1)	—
<i>Apaloderma narina</i>					
Pied Kingfisher	82	—	1 (1)	—	—
<i>Ceryle rudis</i>					
European Bee-eater	55	—	—	1 (1)	—
<i>Merops apiaster</i>					
Hoopoe	57	—	1 (1)	1 (1)	—
<i>Upupa epops</i>					
Scimitar-billed Woodhoopoe	35	—	1 (1)	—	—
<i>Phoeniculus cyanomelas</i>					
Red-billed Hornbill	130	—	—	—	1 (1)
<i>Tockus erythrorhynchus</i>					
Black-collared Barbet	57	—	—	2 (2)	—
<i>Lybius torquatus</i>					
Red-capped Lark	26	—	—	1 (1)	—
<i>Calandrella cinerea</i>					
Chestnut-backed Finchlark	14	—	—	1 (1)	1 (1)
<i>Eremopterix leucotis</i>					
Grey-backed Finchlark	17	—	19 (1)	—	—
<i>E. verticalis</i>					
Unidentified lark	20	—	—	2 (1)	—
European Swallow	18	1 (1)	—	—	—
<i>Hirundo rustica</i>					
Rock Martin	22	1 (1)	4 (4)	—	—
<i>H. fuligula</i>					
Brown-throated Martin	13	—	11 (3)	—	—
<i>Riparia paludicola</i>					

Appendix 1. Continued.

PREY TAXON	AVERAGE MASS (g)	CAPE PENINSULA	ORANGE RIVER	SOUTPANSBERG	
				PEREGRINES	LANNERS
Black-headed Oriole	69	—	—	1 (1)	—
<i>Oriolus larvatus</i>					
Unidentified sylviid	20	—	2 (2)	—	—
Fiscal Shrike	41	—	—	1 (1)	—
<i>Lanius collaris</i>					
Unidentified shrike	60	—	1 (1)	—	—
European Starling—adult	76	68 (9)	—	—	—
<i>Sturnus vulgaris</i>					
European Starling—fledgling	76	5 (3)	—	—	—
Pied Starling	107	1 (1)	—	—	—
<i>Spreo bicolor</i>					
Plum-colored Starling	46	—	—	1 (1)	—
<i>Cinnyricinclus leucogaster</i>					
Cape Glossy Starling	84	—	—	6 (3)	—
<i>Lamprotornis nitens</i>					
Greater Blue-eared Glossy Starling	76	—	—	1 (1)	—
<i>L. chalybaeus</i>					
Unidentified starling	80	—	—	2 (1)	—
Red-winged Starling—adult	135	3 (3)	—	1 (1)	—
<i>Onychognathus morio</i>					
Red-winged Starling—fledgling	135	—	—	1 (1)	—
Pale-winged Starling	107	—	4 (2)	—	—
<i>O. nabouroup</i>					
Unidentified starling	80	—	—	1 (1)	1 (1)
White-browed Sparrow-weaver	48	—	—	3 (3)	1 (1)
<i>Plocepasser mahali</i>					
Sociable Weaver	27	—	1 (1)	—	—
<i>Philetairus socius</i>					
House Sparrow	24	2 (1)	—	—	—
<i>Passer domesticus</i>					
Cape Sparrow	26	10 (3)	4 (3)	4 (3)	2 (2)
<i>P. melanurus</i>					
Cape Weaver	45	7 (4)	—	3 (2)	—
<i>Ploceus capensis</i>					
Masked Weaver	27	1 (1)	1 (1)	—	1 (1)
<i>P. velatus</i>					
Unidentified weaver	35	—	—	1 (1)	1 (1)
Red-billed Quelea	19	—	2 (2)	6 (3)	1 (1)
<i>Quelea quelea</i>					
Red Bishop	23	—	2 (2)	1 (1)	—
<i>Euplectes orix</i>					
Yellow-rumped Widow	45	2 (1)	—	—	—
<i>E. capensis</i>					
Unidentified ploceid	40	1 (1)	1 (1)	—	2 (2)
Common Waxbill	8	—	3 (3)	—	—
<i>Estrilda astrild</i>					
Red-headed Finch	23	—	—	3 (3)	—
<i>Amadina erythrocephala</i>					
Yellow-eyed Canary	13	—	—	1 (1)	—
<i>Serinus mozambicus</i>					

Appendix 1. Continued.

PREY TAXON	AVERAGE MASS (g)	CAPE PENINSULA	ORANGE RIVER	SOUTPANSBERG	
				PEREGRINES	LANNERS
Forest Canary	16	—	—	1 (1)	—
<i>S. scotops</i>					
Bully Canary	26	—	—	—	1 (1)
<i>S. sulphuratus</i>					
Yellow Canary	17	1 (1)	1 (1)	—	—
<i>S. flaviventris</i>					
White-throated Canary	27	—	2 (1)	—	—
<i>S. albogularis</i>					
Unidentified canary	15	1 (1)	—	1 (1)	—
Unidentified fringillid	15	—	1 (1)	1 (1)	1 (1)
Unidentified small birds—adults	20	4 (3)	2 (2)	9 (3)	2 (2)
Unidentified small birds—young	20	1 (1)	—	—	—
Unidentified small-medium birds	60	6 (4)	—	11 (4)	8 (6)
Unidentified medium birds	130	5 (3)	4 (4)	2 (2)	4 (2)
Unidentified very large birds	600	—	—	1 (1)	—
Mammals					
Unidentified shrew	10	—	—	—	1 (1)
Unidentified fruit bat	130	—	—	6 (2)	—
Flat-headed free-tailed bat	14	—	8 (1)	—	—
<i>Sauromys petrophilus</i>					
Egyptian free-tailed bat	15	—	8 (1)	—	—
<i>Tadarida aegyptiaca</i>					
Hildebrandt's horseshoe bat	30	—	—	1 (1)	—
<i>Rhinolophus hildebrandtii</i>					
Unidentified insectivorous bats	15	1 (1)	6 (4)	3 (3)	—
Multimammate mouse	65	—	—	*1 (1)	—
<i>Mastomys natalensis</i>					
Namaqua rock mouse	45	—	*1 (1)	—	—
<i>Aethomys namaquensis</i>					
Small unidentified murid	25	—	—	—	1 (1)
Medium unidentified murid	45	*2 (2)	*3 (3)	*2 (2)	1 (1)
Large unidentified murid	120	—	—	*2 (2)	—
Unidentified squirrel	160	—	—	*1 (1)	—
Small unidentified bovid	5000	—	—	*1 (1)	—
TOTAL		515 (10)	252 (7)	418 (7)	175 (10)

NEST DISPERSION, DIET, AND BREEDING SUCCESS OF BLACK KITES (*MILVUS MIGRANS*) IN THE ITALIAN PRE-ALPS

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ABSTRACT.—We studied a population of Black Kites (*Milvus migrans*) from 1992–96 in a 100-km² study area in the Italian pre-Alps around Lake Lugano. Population density increased from 24 territorial pairs per 100 km² in 1992 to 38 in 1996. Nearest neighbor distances were variable, averaging 1288 m for solitary pairs ($N = 24$) and 306 m for colonial ones ($N = 151$). Regular spacing of nest sites was the rule within colonies, but inter-nest distance for solitary breeders increased as new pairs settled in the area. Nests occurred both in trees (58%, $N = 84$) and on cliffs (42%); 23% and 5% ($N = 84$) of the nests were originally built by Common Buzzards (*Buteo buteo*) and Ravens (*Corvus corax*), respectively. Mean laying date was 25 April ($N = 42$), mean clutch size was 2.29 eggs ($N = 42$) and mean number of fledged young was 0.97, 1.11, and 1.78 young per territorial, reproductive, and successful pairs, respectively ($N = 143, 95, 78$). The percentage of successful territorial pairs was 55% ($N = 143$). Diet was dominated by fish and birds, which accounted for 62% and 28% of 307 identified prey items, respectively. Compared with other European populations, this population showed an intermediate density and an average clutch size but the lowest fledging and breeding success ever recorded for the species. Reasons for the low success were unclear, but may have been related to low food availability or water pollution and consequent pesticide contamination.

KEY WORDS: *Black Kite*, *Milvus migrans*; *coloniality*; *density*; *diet*; *breeding success*; *Italy*.

Dispersion de nidos, dieta, y éxito reproductivo de *Milvus migrans* en los pre-Alpes Italianos

RESUMEN.—Estudiamos una población de *Milvus migrans* desde 1992–96 en un área de 100 kms en los pre-Alpes italianos alrededor del Lago Lugano. La densidad poblacional aumentó de 24 parejas territoriales por 100 kms en 1992 a 38 en 1996. La distancia mas próxima entre vecinos fué variable y promedió 1288 m entre parejas solitarias ($N = 24$) y 306 m entre las parejas coloniales ($N = 151$). Los espacios regulares de los nidos fueron la regla entre las colonias, pero la distancia entre nidos para los reproductores solitarios se incrementó a medida que se asentaron nuevas parejas en el área. Los nidos se encontraron tanto en árboles (58%, $N = 84$) como en riscos (42%), 23% y 5% ($N = 84$) de los nidos fueron originalmente construidos por *Buteo buteo* y *Corvus corax*, respectivamente. La media del día de la puesta fué el 25 de abril ($N = 42$). La media del tamaño de la nidada fué 2.29 huevos ($N = 42$) y la productividad media fué 0.97, 1.11, y 1.78 juveniles por territorio. Las parejas productivas territorialmente exitosas representaron el 55% ($N = 53$). La dieta fue principalmente dominada por peces y aves (62% y 28% respectivamente) de los 307 items de presas identificadas. Al comparar con otras poblaciones europeas, estas poblaciones mostraron una densidad intermedia y una nidada promedio, pero al mismo tiempo el mas bajo éxito reproductivo y reclutamiento registrado para la especie. Las causas de esto, son poco claras y pudieron estar relacionadas con la poca disponibilidad de comida o con la polución del agua y la consecuente contaminación por pesticidas.

[Traducción de César Márquez]

The Black Kite (*Milvus migrans*) is a medium-sized accipitrid that is distributed throughout the Old World and Australasia. It has been defined as an adaptable and opportunistic feeder (Geroudet 1965, Delibes 1975, Arroyo 1978, Jones and Manéz

1990) and as one of the most numerous and successful birds of prey in the world (Brown and Amadon 1968). Despite its local abundance, the Black Kite was recently classified as a declining and vulnerable species in Europe (Viñuela and Sunyer

1994). Although populations were reported to be stable or increasing in western Europe between 1970–90 (e.g., Bustamante and Hiraldo 1993, Doumeret 1995), pronounced decreases have been observed in Portugal, eastern Europe, and Russia during the same period (Viñuela and Sunyer 1994, Bijlsma 1997). Recently, recorded cases of pesticide contamination (Hernandez et al. 1986, Jenni-Eiermann et al. 1996), nest robbing (García Ferré and de Juan 1983) and water pollution (e.g., Ceschi et al. 1996) in the species' core distribution areas point to an urgent need for quantitative monitoring of breeding populations (Viñuela and Sunyer 1994).

In Italy, both local population increases and declines have been reported (Petretti 1992, De Giacomo et al. 1993), but information is fragmentary and mainly nonquantitative (Viñuela and Sunyer 1994). During the 20th century, the species declined dramatically in the Po Plain. For example, one colony in Bosco Fontana, near the city of Mantova, declined from over 100 pairs in the 1930s (Arrigoni degli Oddi and Moltoni 1931) to <10 pairs in the 1970s (Micheli 1990). The largest Italian populations are currently concentrated in the pre-Alps (Micheli 1990). No quantitative estimates of density, diet or productivity have been published for these populations.

In this paper, we report the results of a 5-yr study on a Black Kite population in a pre-Alpine area of northern Italy. The aim of the research was to provide quantitative data on Black Kite density, nest dispersion, colony size, diet and productivity, and to compare them with estimates from other populations.

STUDY AREA

The study area was a 100-km² plot located along the Italian coast of Lake Lugano. It included two pre-Alpine valleys: the Ceresio Valley along the lake and the Ganna Valley further inland from the lake. Altitude ranged from 275–1125 m. The landscape was characterized by pre-Alpine mountains, mainly of sedimentary origin, ranging from 526–1125 m in peak elevation. Mountain slopes were covered by continuous deciduous woodland which accounted for 77% of the study area and was locally interrupted by a few open areas. These open areas resulted from human activities (regular burning or sheep grazing) and were covered by dry grassland, ferns, or various bushes, mainly common hazel (*Corylus avellana*). Dominant tree species included sweet chestnut (*Castanea sativa*), downy oak (*Quercus pubescens*), sessile oak (*Quercus petraea*), European hop-hornbeam (*Ostrya carpinifolia*), and locust (*Robinia pseudoacacia*). Forests were managed for timber production by stool shoot regeneration (cop-

pice system, Matthews 1989) on a 20–30 yr rotation basis. Single mature trees are often kept into the next rotation as seed bearers (coppice with standards system, Matthews 1989). Thus, even though single mature trees were present almost everywhere, most woodlots had been thinned or clearfelled in recent times (<40 yr), resulting in a homogeneous cover of second growth forest. Following the recent decline in coppice management throughout Europe (Matthews 1989), some woodlots were being converted to mature forest; nevertheless, mature woodland was confined to a few steep and often inaccessible slopes.

Cultivated fields, mainly grassland and maize (*Zea mays*) fields, were located on the valley floors and accounted for 3% of the land. Sixteen small villages, all confined to the valley floors, covered 13% of the study area. Thus, except for forestry operations, human activities were mainly confined to lowland and were virtually absent from the mountain slopes. The Lake Lugano water surface accounted for 6% of the study area which also included two smaller lakes (17 and 25 ha); overall, aquatic habitat covered 7% of the study area.

Climate was temperate continental, with wet springs and dry summers (Pinna 1978). Annual rainfall ranged from 1600–2100 mm, with two peaks, one in the spring and one in the autumn, and the former more pronounced than the latter (Belloni 1975).

METHODS

We censused Black Kite nests from 1992–96. The earliest territorial individuals were observed in the study area on 18 March. As soon as kites settled on their breeding territories, they started to perch in highly prominent positions, refurbish nests and carry out conspicuous aerial displays to signal territory ownership or to attract a mate (Viñuela 1993). Nests were censused by progressive, complete searches as new pairs arrived from migration and settled on territories. No pairs settled on territories after the middle of April, when some pairs were already laying eggs. All nests were found during the pre-incubation period, by watching the resident pair's territorial displays and nest material transfers. This also allowed us to census the nonbreeding sector of the territorial population (i.e., pairs that failed to lay eggs).

Nest dispersion was analyzed by means of the G-statistic (Brown 1975), calculated as the ratio of the geometric to the arithmetic mean of the squared nearest neighbor distances (NNDs). Values ranged from 0–1 with values ranging from 0.65–1.00 indicating a regular dispersion of nest sites (Brown 1975). Pairs were defined as solitary when they nested >700 m from their nearest neighbor. However, five nests belonging to two territories were defined as solitary despite having a NND <700 m. These were located on opposite sides of a mountain and the birds could not see their nearest neighbor while in their nest area; also, they were not seen to interact with the neighboring pairs during each of three 1-hr observation sessions during the pre-laying period (see Brown and Brown 1996). Apart from these five cases, all pairs <700 m from their nearest neighbor were defined as colonial, and all interacted regularly with their neighbors, mostly through contests caused by territorial intrusions.

Whenever possible, nest contents were checked three times: first during incubation to assess clutch size, second

Table 1. Density and extent of coloniality in a Black Kite population in the Italian pre-Alps between 1992–96.

VARIABLE	1992	1993	1994	1995	1996
No. of territorial pairs	27	33	35	39	41
Territorial pairs/100 km ²	24	30	32	36	38
No. of colonial pairs (%)	26 (96)	29 (88)	28 (80)	35 (90)	33 (80)
No. of colonies	6	6	6	7	5

just after hatching to estimate hatching success, brood size, and date of hatching, and third, when the nestlings were 40–45 d old to record the number of young raised (nestlings fledge at about 48 d old, Bustamante and Hiraldo 1993). We checked nest contents by climbing the nest tree, going down the nesting cliff with a rope or simply watching the nest cup from a distant vantage point with binoculars or a 20–60× telescope. To minimize disturbance, risk of desertion or nest predation by Ravens (*Corvus corax*), only nests that could be checked very rapidly were visited during incubation or early hatching. Thus, clutch size, laying date and number of laying pairs were assessed from a subsample of nests. Hatching date was calculated by backdating from the feather development of nestlings first observed when <15 d old and by comparison to reference information in Richard (1934), Cramp and Simmons (1980) and Hiraldo et al. (1990). Laying date was estimated by subtracting 29 d, the average incubation period (Viñuela 1993), from hatching date. Additional data were collected from a loose colony of three pairs 3 km from the border of the study area.

We collected prey remains found under nests during each nest visit and identified them to the genus or species level assuming the smallest possible number of individuals. Fish scales were identified following Steinmetz and Müller (1939) and Baliglinière and Le Louarn (1987); other vertebrate remains were identified by comparison to a reference collection.

Terminology followed Steenhof (1987) with a reproductive pair being one which laid eggs, a successful pair being one which raised at least one young until it was 40 d old and breeding success being the percentage of successful territorial pairs. Raptors generally nest in traditional nest areas year after year (Newton 1979); a nest area was defined as an area where more than one nest was found in the same or in different years, but where only one pair nested each year.

Stepwise logistic regression analysis (Norusis 1993) was employed to analyze among year differences in the probability of territorial pairs laying eggs and of eggs hatching. Logistic regression uses a linear combination of independent variables to explain the variance of a dependent dichotomous variable. To meet the assumptions of normality, NNDs were always log transformed prior to parametric tests. Means are given with ± 1 SE. All tests were two-tailed and statistical significance was set at $P < 0.05$.

RESULTS

Density and Nest Dispersion. The number of territorial pairs increased steadily from 27 in 1992 to

41 in 1996. Density correspondingly increased from 24 to 38 territorial pairs per 100 km² (Table 1). The loose colony outside the study area contained 3 pair in each of the five study years. The number of nest areas censused was 48. Of these, six were always occupied by solitary pairs, 37 by colonial pairs and five by pairs that switched from colonial to solitary nesting ($N = 3$), or *vice versa* ($N = 2$), during the study period. Territorial behavior was intense within 50–200 m of nests but was rarely observed at foraging areas.

The number of colonies censused was stable and ranged from five to seven. Colonies contained on average 5.0 nests (± 0.6 , $N = 30$). The percentage of colonial pairs ranged from 80–96% (Table 1). In particular, the number of pairs in large colonies (>5 pair) did not increase significantly through the years ($\chi^2 = 2.12$, $df = 4$, $P = 0.710$). Instead, the number of pairs in small colonies (≤ 4 pair) progressively decreased ($\chi^2 = 9.76$, $df = 4$, $P = 0.040$), except in 1995 (Fig. 1) when a new two-pair colony was created by settlement by a new pair near a previously solitary pair. The percentage of solitary pairs did not increase significantly over time ($\chi^2 = 4.92$, $df = 4$, $P = 0.301$, Fig. 1).

Mean NND was 306 m for colonial pairs (± 13.7 , $N = 151$) and 1288 m for solitary pairs (± 166 , $N = 24$). NNDs ranged from 60–690 m for colonial pairs and from 450–4250 m for solitary pairs. Mean NND of solitary pairs did not increase through the years (Kruskal-Wallis $\chi^2 = 1.95$, $df = 3$, $P = 0.583$, Table 2). For three large colonies (A, B, and C, Table 2), we tested the effect of year and colony on nest spacing by means of a two-way ANOVA: the interaction of year and colony was almost significant (partial $F_{8,98} = 1.86$, $P = 0.076$) and both year and colony significantly affected mean NND independently (respectively: partial $F_{4,98} = 11.01$, $P = 0.000$; partial $F_{2,98} = 20.78$, $P = 0.000$). Variation in NND within colonies among years was mainly caused by the progressive increase in territorial pairs in two colonies around the lake. New pairs

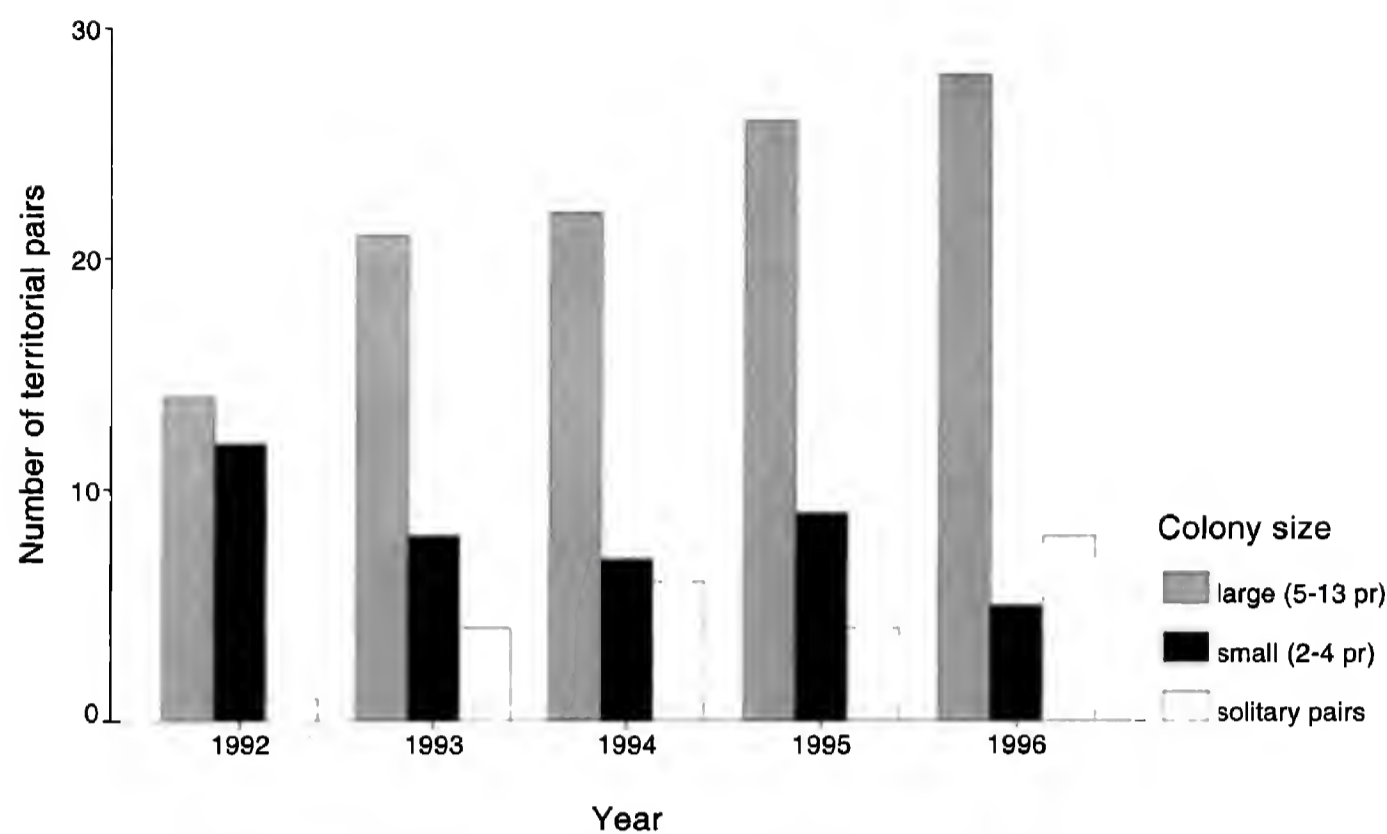


Figure 1. Number of Black Kite pairs breeding solitarily or in small (≤ 4 pairs) and large (≥ 5 pairs) colonies between 1992–96 in the Italian pre-Alps.

Table 2. Mean (\pm SE) Black Kite nearest neighbor distances for 24 solitary pairs and at seven colonies in the Italian pre-Alps between 1992–96.

NEST TYPE	MEAN NEAREST NEIGHBOR DISTANCE (m)					
	1992	1993	1994	1995	1996	1992–96
Solitary		934 \pm 161 (4) ^a 0.82 ^b	1203 \pm 199 (7) ^a 0.72 ^b	1304 \pm 332 (4) ^a 0.68 ^b	1508 \pm 437 (8) ^a 0.38 ^b	1288 \pm 166 (24) ^a 0.54 ^b
Colony A	394 \pm 40 (7) ^a 0.88 ^b	373 \pm 64 (8) ^a 0.67 ^b	288 \pm 49 (9) ^a 0.64 ^b	252 \pm 28 (12) ^a 0.79 ^b	241 \pm 33 (13) ^a 0.68 ^b	295 \pm 20 (49) ^a 0.67 ^b
Colony B	292 \pm 12 (7) ^a 0.96 ^b	169 \pm 24 (8) ^a 0.67 ^b	(7) ^a 0.89 ^b	167 \pm 15 (9) ^a 0.87 ^b	150 \pm 25 (8) ^a 0.67 ^b	183 \pm 10 (39) ^a 0.78 ^b
Colony C	679 \pm 24 (3) ^a 0.10 ^b	355 \pm 51 (5) ^a 0.85 ^b	290 \pm 23 (5) ^a 0.95 ^b	237 \pm 44 (5) ^a 0.75 ^b	174 \pm 23 (7) ^a 0.83 ^b	307 \pm 34 (25) ^a 0.59 ^b
Colony D	597 \pm 27 (3) ^a 0.99 ^b	597 \pm 27 (3) ^a 0.99 ^b	567 \pm 37 (3) ^a 0.98 ^b	567 \pm 37 (3) ^a 0.98 ^b	433 \pm 123 (3) ^a 0.74 ^b	552 \pm 29 (15) ^a 0.92 ^b
Colony E	401 \pm 3 (3) ^a 0.10 ^b	317 \pm 45 (3) ^a 0.93 ^b	640 \pm 0 (2) ^a	640 \pm 0 (2) ^a	640 \pm 0 (2) ^a	500 \pm 44 (12) ^a 0.83 ^b
Colony F	213 \pm 10 (3) ^a 0.99 ^b	206 \pm 0 (2) ^a	206 \pm 0 (2) ^a	206 \pm 0 (2) ^a		208 \pm 3 (9) ^a 0.99 ^b
Colony G				403 \pm 0 (2)		403 \pm 0 (2)
All nests	430 \pm 58 (27) ^a	394 \pm 48 (33) ^a	492 \pm 75 (35) ^a	388 \pm 63 (39) ^a	493 \pm 115 (41) ^a	441 \pm 36 (175) ^a

^a Sample size.
^b G statistic.

settling in these colonies did not place their nests in the outer parts of colonies or far away from traditional pairs, but selected areas near already-occupied nests. Thus, mean within-colony NND decreased as the number of pairs in the colonies increased though the years (colony A: $F_{4,44} = 2.64$, $P = 0.046$; colony C: $F_{4,20} = 11.29$, $P = 0.000$, Table 2). Mean NND did not vary significantly with time in colony C, where the number of pairs remained stable through the years ($F_{4,34} = 2.07$, $P = 0.106$). Due to this, NNDs are shown separately for each colony in Table 2.

The G-statistic declined progressively for solitary pairs through the years, indicating a regular dispersion of nest sites between 1993–95, but not in 1996 (Table 2). Pooling years, the overall dispersion of solitary nests was not regular ($G = 0.540$), probably because of the progressive increase in the mean NND of solitary nesters over time. Instead, the G-statistic indicated a regular dispersion of nest sites within 22 of 23 colonies with ≥ 3 pairs.

Nest Sites. All territorial pairs built nests ($N = 175$ pairs in 48 nest areas). After settling on territories, most pairs brought nest material to one nest, but 13 pairs in six nest areas brought material to two nests during the beginning of the pre-laying period, before selecting the nest in which they eventually laid eggs. Altitude of the nest sites ranged from 240–870 m, averaging 515 m (± 14 , $N = 175$). The 175 censused territorial nestings took

place in 84 different nest structures, each one occupied for one to five consecutive years ($\bar{x} = 2.1 \pm 0.1$, $N = 84$).

Of these nests, 58% were placed in trees while the remainder were on cliffs ($N = 84$). Of 49 tree nests, 39% were in sweet chestnut, 33% in sessile or downy oak, 18% in locust, 6% in European hop-hornbeam, 2% in common lime (*Tilia europaea*), and 2% in Scotch pine (*Pinus silvestris*) trees. The 35 cliff nests were placed on bare rock ledges (29%) and at the base (54%) or in the canopy (17%) of trees, generally downy oaks, growing on cliff faces. Many pairs used nest structures originally built by other species, to which they added new material: 23% of 84 occupied nest structures were originally built by Common Buzzards (*Buteo buteo*) and 5% were old Raven nests. Some nests were being used by the original occupants when they were taken over by Black Kites. Buzzard nests were taken over during the original owners' pre-laying period and one Raven nest still contained nestlings when it was occupied by kites, which preyed on the chicks before starting to add new material to the nest.

Breeding Season. There were no year-to-year differences in mean laying date ($F_{4,40} = 0.68$, $P = 0.762$, Table 3). Laying dates ranged from 12 April–8 May, averaging 25 April (Table 3). No cases of replacement clutches in the same nest were observed after breeding failures, even when these

Table 3. Mean (\pm SE) laying date and productivity estimates of an Italian pre-Alpine Black Kite population between 1992–96.

VARIABLE	1992	1993	1994	1995	1996	1992–96
Laying date in April	24.6 \pm 1 (7) ^a	23.3 \pm 2 (7) ^a	25.5 \pm 2 (8) ^a	28.7 \pm 3 (9) ^a	25.3 \pm 2 (14) ^a	25.6 \pm 1 (45) ^a
Territorial pairs ^b						
% reproductive	17	31	31	33	31	143
Pairs (N)	100 (17) ^a	76 (21) ^a	86 (22) ^a	86 (21) ^a	74 (19) ^a	84 (100) ^a
Clutch size (N)	2.5 \pm 0.2 (10) ^a	2.5 \pm 0.2 (11) ^a	1.8 \pm 0.3 (8) ^a	1.8 \pm 0.4 (5) ^a	2.6 \pm 0.2 (8) ^a	2.3 \pm 0.1 (42) ^a
% hatching success	68 (25) ^c	89 (27) ^c	79 (14) ^c	89 (9) ^c	100 (21) ^c	84 (96) ^c
% successful pairs	71	58	48	42	61	55
Young fledged per territorial pair	1.06 \pm 0.2	1.16 \pm 0.2	0.71 \pm 0.2	0.67 \pm 0.2	1.32 \pm 0.2	0.97 \pm 0.1
Young fledged per reproductive pair	1.00 \pm 0.2 (16) ^a	1.24 \pm 0.2 (21) ^a	0.86 \pm 0.2 (21) ^a	0.76 \pm 0.2 (21) ^a	1.72 \pm 0.3 (18) ^a	1.11 \pm 0.1 (97) ^a
Young fledged per successful pair	1.50 \pm 0.2 (12) ^a	2.00 \pm 0.2 (18) ^a	1.47 \pm 0.2 (15) ^a	1.57 \pm 0.2 (14) ^a	2.16 \pm 0.2 (19) ^a	1.78 \pm 0.1 (78) ^a

^a Sample size (when different from that in column "territorial pairs").
^b Those checked for nesting success.
^c Number of eggs. Sample size of nests same as for clutch size.

Table 4. Diet of breeding Black Kites in the Italian pre-Alps (1992–97), as estimated by food remains collected under nests.

PREY CATEGORY	NUMBER OF ITEMS (%)
Fishes	190 (61.9)
Rudd (<i>Scardinius erythrophthalmus</i>)	59 (19)
Chub (<i>Leuciscus cephalus</i>)	56 (18)
Unidentified Ciprinidae	37 (12)
Others ^a	38 (12)
Birds	85 (27.7)
Blackbird (<i>Turdus merula</i>)	20 (7)
Others ^b	65 (21)
Unidentified Passeriformes	20 (7)
Mammals	24 (7.8)
Unidentified Microtidae	15 (5)
Others ^c	9 (3)
Reptiles ^d	5 (1.5)
Amphibians ^e	1 (0.3)
Invertebrates ^f	2 (0.7)
Total	307

^a Includes: perch (*Perca fluviatilis* $N = 13$), bleak (*Alburnus albidus alborella*, $N = 11$), roach (*Rutilus rutilus*, $N = 8$), pumpkinseed (*Lepomis gibbosus*, $N = 4$), large-mouth black bass (*Micropterus salmoides*, $N = 2$).

^b Includes: Rock Dove (*Columba livia*, $N = 11$), Starling (*Sturnus vulgaris*, $N = 6$), Jay (*Garrulus glandarius*, $N = 5$), Italian Sparrow (*Passer domesticus italiae*, $N = 4$), Black Kite nestling ($N = 2$), Honey Buzzard nestling (*Pernis apivorus*, $N = 2$), Tawny Owl (*Strix aluco*, $N = 2$), Hooded Crow (*Corvus corone cornix*, $N = 2$), Song Thrush (*Turdus philomelos*, $N = 2$), Moorhen (*Gallinula chloropus*, $N = 1$), Collared Dove (*Streptopelia decaocto*, $N = 1$), Barn Swallow (*Hirundo rustica*, $N = 1$), House Martin (*Delichon urbica*, $N = 1$), Chaffinch (*Fringilla coelebs*, $N = 1$), Great Tit (*Parus major*, $N = 1$), Reed Bunting (*Emberiza schoeniclus*, $N = 1$).

^c Includes: dormouse (*Myoxus glis*, $N = 3$), common mole (*Talpa europaea*, $N = 3$), rabbit (*Oryctolagus cuniculus*, $N = 2$), unidentified mammal from slaughterhouse ($N = 1$).

^d Includes: Aesculapian snake (*Elaphe longissima*, $N = 2$), unidentified Colubridae ($N = 3$).

^e Includes: *Rana* spp. ($N = 1$).

^f Includes: *Cetonia* spp. ($N = 2$).

happened early in incubation. All nestlings fledged by 15 July and all Black Kites departed the study area by 10 August each year.

Productivity. Each year, 74–100% of territorial pairs laid eggs (Table 3), with no clear trend over time. Year did not enter a stepwise logistic regression model with laying or nonlaying of eggs as a dependent variable. The overall mean number of laid eggs ($\bar{x} = 2.3$, $N = 42$) varied significantly among years ($F_{4,37} = 2.75$, $P = 0.043$) and was significantly lower in 1994 than in 1992, 1993, and 1995 (Duncan’s Multiple Range Test, $P < 0.05$, Ta-

ble 3). On the whole, 84% of 96 eggs checked hatched. Stepwise logistic regression analysis showed a significant effect of year on probability of egg hatching ($B = 0.65$, Wald = 5.88, $df = 1$, $P = 0.015$, reclassification rate = 84%).

The number of young fledged per territorial pair averaged 0.97 ($N = 143$) and differed significantly among years ($F_{4,138} = 2.49$, $P = 0.045$). Productivity was significantly higher in 1996 than in 1994 and 1995 (Duncan’s Multiple Range Test, $P < 0.05$, Table 3). Significant among-year differences also were detected for mean number of fledged young per reproductive pair ($F_{4,92} = 2.68$, $P = 0.036$). Again, average values were significantly higher in 1996 than in 1994 and 1995 (Duncan’s Multiple Range Test, $P < 0.05$, Table 3). Mean number of fledged young per successful pair was 1.78 ($N = 78$) and also varied among years ($F_{4,73} = 3.69$, $P = 0.009$), with more young fledged on average in 1996 than in 1992, 1994, and 1995 and in 1993 than in 1994 (Duncan’s Multiple Range Test, $P < 0.05$, Table 3). Finally, the percentage of successful territorial pairs in the population ranged from 42% in 1995 to 71% in 1992, with no significant among-year differences ($\chi^2 = 4.98$, $df = 4$, $P = 0.301$, Table 3).

Sample size allowed us to test the effect of year and colony on mean number of fledged young in three colonies (A, B, and C) by means of a two-way ANOVA. The effect of the interaction between year and colony on mean number of young fledged per territorial pair was significant (partial $F_{8,83} = 3.01$, $P = 0.005$), but only approached significance when using mean number of fledged young per reproductive pair or per successful pair as the dependent variable (respectively: partial $F_{8,66} = 1.80$, $P = 0.092$; partial $F_{6,42} = 1.96$, $P = 0.093$). In these two cases, colony was the only significant main effect (respectively: partial $F_{2,66} = 3.32$, $P = 0.042$; partial $F_{2,42} = 3.54$, $P = 0.038$). These patterns were mainly caused by the productivity of colony C, where fledging success remained similar to that in other colonies until 1995, when no young were raised in any of the eight nests checked. In 1996, only one young was raised in seven nests checked in colony C. The reason for such a dramatic decline in productivity was not clear.

Overall, causes of breeding failure were seldom identified: 89% of failures occurred during incubation ($N = 19$) and the rest occurred during the early part of the fledging period. Probable causes of failure included: failed hatching of eggs and

Table 5. Nesting density of Black Kite populations in Europe, 1966–96.

AREA (PERIOD)	HABITAT	(N)	DENSITY (pr/100km ²)	NEAREST NEIGHBOR DISTANCE (N)	REFERENCE
Matas Gordas, Spain (1987–89)	Grassland and marshland	21–45	700–1500		Viñuela et al. 1994
Rhône Plain, France (1970)	River plain	140	609		Sermet 1980
Doñana, Spain (1981–84)	Marshland	80	266.6	206 (47) ^a	Hiraldo et al. 1990
Lac Lemán, Switzerland (1975–90)	Farmland and lake	319	100.6		Henrioux and Henrioux 1995
Neuchâtel, Switzerland (1968)	Farmland and lake	337	69.6		Sermet 1980
Lorraine, France (1966)	Woodland and pas- ture	66	44.6		Thiollay 1967
Lake Lugano, Italy (1992– 96)	Woodland and lake	27–41	24–38	441 (175)	This study
Castelporziano, Italy (1991– 92)	Woodland and farmland	16	33.3	103 (16)	De Giacomo et al. 1993
Lake Constance, Germany (1968–69)	Farmland and lake	25–30	18.5–22.2		Heckenroth 1970
Limousin, France (1976– 78)	Bocage ^b	21	9.5		Nore 1979
Drömling, Germany (1993– 94)	Farmland	8	7.02	2330 (8) ^c	Seelig et al. 1996
Monti della Tolfa, Italy (1973–80)	Woodland and pas- ture	42	4.9		Petretti and Petretti 1981
Brandenburg, Germany (1979)	Farmland	215	0.74		Fiuczynski 1981

^a Estimate from Bustamante and Hiraldo (1990), for the period 1985–88.
^b Pasture and woodland enclosed by stone walls or hedges.
^c Calculated from the published map.

consequent desertion (three cases), predation (two cases) and disturbance by rock climbers (one case).

Diet. Fish and birds dominated the diet and accounted for 61.9% and 27.7% of 307 identified prey items, respectively (Table 4). Mean length of 15 fish found uneaten in nests was 18.6 cm (±1.8, range = 7–30 cm). Of 54 avian prey items, 26% were juveniles.

DISCUSSION

The number of territorial pairs of Black Kites increased steadily during our study. It is difficult to say whether this was caused by a real population increase or a simple population fluctuation. Spatial and temporal variations in Black Kite population density and productivity have been reported by many authors (Fiuczynski and Wendland 1968, Viñuela et al. 1994, Doumeret 1995, Bijlsma 1997).

Results of the analyses on NND and fledging success in the three large colonies showed that each colony could be considered a separate unit within the population. Each colony was characterized by its own nest spacing distance, which tended to be regular, but which differed from that of other colonies and sometimes varied from one year to the next. Similarly, productivity varied among colonies within and among years within each colony. These results emphasized the importance of monitoring populations composed of more than just one colony for as many years as possible to obtain an unbiased estimate of density, nest dispersion, and productivity. To date, many studies on Black Kites have been conducted in just one colony or in areas of homogeneous high density that are functionally similar to one large colony (e.g., Desai and Malhotra 1979, Koga et al. 1989, Viñuela et al. 1994).

Overall, the population showed remarkable op-

Table 6. Productivity of Black Kite populations in Europa and Asia, 1966–96.

AREA (PERIOD)	HABITAT	N	HATCHING		
			CLUTCH SIZE	SUCCESS ^a (EGGS)	BREEDING SUCCESS
Doñana, Spain (1987–89)	Marshland	166			92%
Germany (1992–95)		599			79%
Nagasaki, Japan (1983–86)	Fishing port	32	2.18 (28) ^b	79% (61) ^b	75%
Limousin, France (1976–78)	Bocage ^d	22			68%
Berlin, Germany (1940–79)	Farmland	215			62%
Lake Lugano, Italy (1992–96)	Woodland and lake	143	2.29 (42) ^b	84% (96) ^b	55%
Slovakia (1975–89)		162	2.98 (44) ^b		
Lac Leman, Switzerland (1975–90)	Farmland and lake	165	2.25		
Lorraine, France (1966)	Woodland and pasture	66	2.26 (45) ^b		
New Delhi, India (1973–76)	Urban	45	2.3 (60) ^b	55% (102) ^b	

^a Data on hatching success not shown in table: 75% (*N* = 36 eggs from 14 nests, Hakel, Germany, 1957; Stubbe 1961) and 64% (*N* = 28 eggs from 10 nests, Mazio, Italy, date unknown; Petretti 1992).
^b Sample size (when different from that in column “*N*”).
^c Data also from Mammen and Stubbe (1995, 1996).
^d Pasture and woodland enclosed by stone walls or hedges.

portunism and elasticity. First, variability in the extent of coloniality between and within years was paralleled by high flexibility in NNDs, the highest observed NND being 70 times greater than the lowest one. Interestingly, as the population increased over the years, new pairs settling in large colonies positioned their nests near existing pairs, possibly as a result of conspecific attraction (Stamps 1988), as was also reported by Viñuela et al. (1994). Advantages of nesting near traditional older pairs (Viñuela 1993) could include local enhancement (Hagan and Walters 1990), information parasitism (e.g., Green 1987) and greater opportunities for kleptoparasitism (Viñuela et al. 1994). The opposite trend was recorded for solitary pairs whose NNDs increased as new pairs colonized the area, suggesting pronounced overall variations in individual pairs nest dispersion, probably in relation to food distribution (Newton 1979, Viñuela et al. 1994).

Second, Black Kite nests were found in a variety of situations: in mature and young trees, within large forests, in small clumps of two or three trees, in isolated trees and on large (>100 m high) and small (<20 m high) cliffs. Nests originally built by other species, especially Common Buzzards, also were occupied readily and taken over by persistent harassment of the original occupants. Cliff nesting,

which is very common all over the Italian pre-Alps, is very rare elsewhere in the Black Kite's range (Cramp and Simmons 1980) and only locally reported in Sicily (Massa 1985), in an area of central Spain (Blanco 1997) and near some Swiss lakes (Sermet 1980).

Finally, diet was dominated by fish and birds on a numeric basis. However, all vertebrate classes and some occasional invertebrate prey were also represented. This finding agreed with the common definition of Black Kites as opportunistic feeders with local specialization in the most available prey (Delibes 1975, Arroyo 1978, Viñuela and Veiga 1992, Blanco 1997).

Despite the overall opportunism and adaptability, productivity estimates for our study population were remarkably low when compared to other published estimates in Europe, Japan and India (Table 5). Nesting densities across Europe were highest near large wetlands and intermediate or very low in farmed or extensive livestock rearing landscapes. Preference for proximity to large wetlands and higher densities near water bodies have been reported by many authors (Heckenroth 1970, Delibes 1975, Hiraldo et al. 1990, Henrioux and Henrioux 1995). Density in the Italian pre-Alpine area was much lower than that of populations near large wetlands (Sermet 1980, Hiraldo et al. 1990,

Table 6. Extended.

MEAN NUMBER OF FLEDGED YOUNG			
TERRITORIAL PAIR	BREEDING PAIR	SUCCESSFUL PAIR	REFERENCE
1.77		1.92 (153) ^b	Jones and Manez 1990
1.63		2.07 (471) ^b	Gedeon 1994 ^c
1 00	1.14 (28) ^b	1.33 (24) ^b	Koga et al. 1989
	1.32	1.93 (15) ^b	Nore 1979
1 20		1.90 (133) ^b	Fiuczynski 1981
0.97	1.1 (95) ^b	1.78 (78) ^b	This study
	2.31		Danko 1989
	2.02		Henrioux and Henrioux 1995
1.32	1.58 (55) ^b		Thiollay 1967
0 98			Desai and Malhotra 1979

Viñuela et al. 1994, Henrioux and Henrioux 1995). It was similar to that along Lake Constance in the 1960s and in low intensity farmland with scattered wetlands (Heckenroth 1970, Thiollay 1967, Seelig et al. 1996), but higher than that in farmed or pasture habitats with few wetlands (Nore 1979, Fiuczynski 1981, Petretti and Petretti 1981). Thus, the observed density was intermediate, but low, compared with other populations near large lakes or wetlands.

Clutch size was similar to that of other populations (Table 6) and hatching success also was comparable to that of other published estimates, except the one of New Delhi, although all of these data were from studies conducted outside Europe or during the pesticide era (1960–70s; Newton 1979). In contrast, the percentage of successful pairs and mean number of fledged young per territorial, reproductive, or successful pair were the lowest ever recorded in Europe and similar only to those in India and Japan. Reasons for such low natality were unclear. During the 1960s, trapping and persecution were common practice in the county of the study area. For example, Bianchi et al. (1969) reported gamekeepers killing 22 Black Kites in one month in a 1-km² area. However, this practice now is rare and we observed no cases of nest robbing, trapping, or persecution. Clutch and nestling predation was minimal, as important potential predators such as Goshawks (*Accipiter gentilis*) and Eagle Owls (*Bubo bubo*) were very scarce in the study area. Thus, the remaining potential caus-

es of low natality could be low food availability or water pollution and consequent prey contamination. DDT contamination of water and fish contamination was reported recently in nearby Lake Maggiore (Ceschi et al. 1996). Even though lake eutrophication and pollution could benefit this species by providing dead or moribund fish (Geroudet 1965, Bijeleveld 1974, Doumeret 1995), pesticide contamination clearly can be harmful for Black Kites (e.g., Jenni-Eiermann 1996, Bijlsma 1997) causing low natality and eventual population decline in the long term. The aim of current and future research on Black Kites in northern Italy is to monitor pesticide concentrations in eggs, population density and productivity levels in different lakes and correlate them with levels of pollution in water and fish prey. There is need for studies assessing the level of water contamination above which toxic chemicals concentrations start to be harmful, both for Black Kites and their fish prey. More published estimates of density and productivity, especially hatching success, are also needed from other European countries.

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STATUS OF NESTING BALD EAGLES IN ARIZONA

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ABSTRACT.—A small, isolated population of Bald Eagles (*Haliaeetus leucocephalus*) breeds along the desert rivers of central Arizona. The extent to which it followed the continental pattern of decline during the DDT era cannot be known because of the paucity of data before 1970 but, from 1970–93 the number of known breeding pairs increased from two to 34. Some of this growth was an artifact of increased surveys, but much was real. During 1987–93, territory occupancy rate was 90%, a higher than normal value for the species, but nest success (45%) and productivity (0.69 young per occupied site, SE = 0.08) were lower than reported for other populations in the coterminous U.S. Much of the annual variation in nesting success and productivity resulted from heat stress and flooding, factors that impacted many breeding areas simultaneously. We recorded 41 breeder fatalities or replacements during 262 monitored breeder/years, and additional fatalities and replacements likely went unrecorded. If replacements equated to fatalities, estimated maximum annual breeder survival was 0.84 (95% C.I. 0.78–0.88), a lower value than elsewhere estimated. Of 131 monitored pairings during the seven years of our research, 24 (18%) contained subadults. This higher than normal rate for Bald Eagles suggests a paucity of floaters (non-territorial adults), although other factors may be involved. Notwithstanding these suggestions of reduced demographic potential, a continuing upward trend in the number of territories is apparent.

KEY WORDS: Bald Eagle; *Haliaeetus leucocephalus*; Arizona; nesting; population status; productivity; breeder turnover; subadult recruitment.

El estatus de águilas calvas anidando en Arizona

RESUMEN.—Una pequeña y aislada población de águilas calvas (*Haliaeetus leucocephalus*) se reproduce a lo largo de los ríos del desierto en el centro de Arizona. Hasta donde está población siguió el patrón continental de disminución poblacional durante la era del DDT, no se ha podido comprobar debido a la falta de información existente antes de 1970. Entre 1970–93 el número de parejas reproductivas conocidas aumentó de dos a 34. Parte de este aumento fue sobreestimado. Durante 1987–93 la tasa de ocupación del territorio fue del 90%, un valor mayor del normal para la especie, el éxito de anidación fue del 45% y la productividad de 0.69 juveniles por sitio ocupado, SE = 0.08; Lo cual fue mas bajo que lo reportado para otras poblaciones de Estados Unidos. Estas variaciones fueron atribuidas al impacto del estrés causado simultáneamente por el calor y las inundaciones en varios sitios de reproducción. Registramos 41 fracasos de los reproductores o remplazos en 262 monitoreos de reproducción por año. Creemos que hubo mas fracasos que no pudieron ser registrados. Si los remplazos fueron iguales a los fracasos, la sobrevivencia anual de reproducción fue de 0.84 (95% C.I. 0.78–0.88), un valor mas bajo de lo estimado en otros lugares. De las 131 parejas monitoreadas durante los 7 años de nuestra investigación, 24 (18%) contenían individuos subadultos. Estas cifras son mas altas de lo normal para las águilas calvas. Lo anterior pudo ser ocasionado por el estancamiento de los individuos “floaters” (adultos sin territorio), aunque otros factores pudieron ser los causantes de esta situación. A pesar de esto y sin subestimar esta situación de reducido potencial productivo, se observa una tendencia creciente de territorios ocupados.

[Traducción de César Márquez]

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Figure 1. The distribution of breeding Bald Eagles in Arizona.

Arizona supports a nesting population of Bald Eagles (*Haliaeetus leucocephalus*) primarily along the Salt and Verde Rivers in the central part of the state (Fig. 1). This small population is somewhat isolated from other centers of breeding activity and occupies habitat drier, warmer, and less vegetated than is typical for the species. Large trees are scarce along the desert rivers and many pairs use cliff nests. The population has been classified as threatened by the U.S. Fish and Wildlife Service (USFWS 1995), and there is concern that the rapidly increasing human population in Arizona may impact its numbers. Herein, we summarize data on occupancy and productivity, and discuss factors affecting survival and recruitment. Drawing upon historical records and reports, and upon field data obtained during 1987–93, we examine the evidence for population self-sustainability.

HISTORY OF OCCURRENCE

When the USFWS began monitoring nesting Bald Eagles in Arizona in 1970, only two occupied territories were known, both on the Verde River (Rubink and Podborny 1976). From 1970–93, the number of known territories increased to 34. To what extent this increase resulted from greater

numbers of eagles is unknown, although it was clear that many territories had been newly established. Others may have been long occupied and simply found by greater search efforts and more extensive surveys, an uncertainty that has affected studies of other populations (Sprunt et al. 1973, Henny and Anthony 1989, Frenzel 1991). Newly discovered sites we examined often contained numerous old nests, but whether these were recently occupied or were remnants of many years past could not be determined since stick nests on cliffs in Arizona may persist for many decades.

Also uncertain, because of the paucity of data before 1972, is the extent to which the Arizona population followed the continental pattern of decline during the DDT era. DDT was applied extensively to cotton and vegetable crops in Arizona and adjacent regions, and the highest DDE levels recorded during the 1967–79 National Starling Monitoring Program were from nearby Maricopa, Arizona and Chaves, New Mexico (Hunt et al. 1986). Prey fish probably contained very little DDE because relatively few farms existed within the drainages occupied by breeding eagles; however, migratory and nomadic waterbirds were likely contaminated.

There is evidence for the existence of a nesting population of Bald Eagles in Arizona prior to 1970. Early sightings of individual eagles were reported by Coues (1866), Henshaw (1875), Willard (1916) and Hargrave (1939). Mearns (1890) described the first breeding record, a tree nest near Stoneman's Lake on the Mogollon Plateau. Bent (1937) reported breeding pairs at Fort Whipple and the Salt River Bird Reservation, an area flooded by Roosevelt Reservoir in 1911. According to Jenks and Stevenson (1937), Bald Eagles bred in the White Mountains and were resident in central eastern Arizona, primarily in the Transition and Upper Sonoran zones. Cited records of two nests in saguaro cacti (*Cereus giganteus*) on the lower Verde River in 1937 and a nesting pair on the Little Colorado River in 1951. Phillips et al. (1964) reported nesting records from the 1930–60s on the Salt and Verde rivers, including pairs breeding during 1930–36 near Saguaro Reservoir (constructed during 1928–30), since the early 1940s near Bartlett Reservoir (completed in 1939), and in the free-flowing Salt River Canyon in 1935, 1944, and 1949. C. McCollough (field notes) observed nesting on the Tonto Arm of Roosevelt Reservoir from 1951–55.

Rubink and Podborny (1976) described a nest on the upper Verde River in the 1960s and a pair near the mouth of the Verde River in 1968. L. Forbis (U.S. Forest Service, unpublished interview with F. Thompson 1979) noted three nests on the upper Verde River occupied during the early- to mid-1960s. G. Gibbons (pers. comm.) observed nesting at Canyon Reservoir on the Salt River in the 1950s and 1960s.

STUDY AREA

In Arizona, Bald Eagles breed mainly in open, desert landscapes of the Upper and Lower Sonoran Life-Zones (Lowe 1964) at elevations ranging from 329–1719 m. Annual precipitation averages from 39 cm at higher elevations to 25 cm in desert scrub habitats, where temperatures may reach 50°C. Livestock grazing, particularly during the close of the 19th century, created conditions leading to extreme loss of soils and vegetation, including formerly extensive riparian forests (Hayden 1965, Hastings 1959, Hastings and Turner 1965, Davis 1982). The resulting need for flood control and water storage prompted the construction of dams in the early 1900s (Hayden 1965). Considerable human recreational activity occurs along the water courses. Some Bald Eagle territories are easily accessible, while others are in remote canyons.

Reservoirs and riverine sections contain both native and introduced fishes. Species most commonly eaten by Bald Eagles are catfish (*Ictalurus punctatus* and *Pylodictis olivaris*), sucker (*Catostomus clarki* and *C. insignis*), common carp (*Cyprinus carpio*), and perciforms (*Pomoxis nigromaculatus*, *Morone mississippiensis* and *Micropterus salmoides*) (Haywood and Ohmart 1986, Grubb 1995, Hunt et al. 1992). Of those listed, only the suckers are native to Arizona. In winter, waterfowl are important prey of the breeding population, especially at reservoirs.

METHODS

During 1987–93, we collected occupancy and reproductive data both on foot and by monthly helicopter flights throughout the breeding season (January–June). Data recorded during the flights included the number of adults seen, location of new nests, number of nestlings and their approximate age. At many territories, nest wardens of the Arizona Bald Eagle Nest Watch Program (ABENWP) reported the exact dates of egg laying, hatching and fledging, and recorded observations of disturbance and fatalities (Forbis et al. 1985). Status terminology followed Postupalsky (1974). Using techniques described in Hunt et al. (1992) and Jackman et al. (1993, 1994), we radiotagged 15 juveniles, eight subadults and 12 breeders at 10 territories. We monitored survival of radio-tagged eagles by airplane. Breeder replacement was determined on the basis of identifying characteristics (e.g., bands on right versus left tarsi, adults preceding subadults, and known deaths of unmarked pair members [Gould and Fuller 1995]). Except in cases where our activities might have jeopardized nestling survival, we entered all occupied nests during 1987–93 and banded all eaglets surviving to 6 wk of age ($N = 119$) with standard

USGS tarsal bands and similarly-sized, color-anodized aluminum visual identification (VID) bands engraved with various symbols.

We recorded standard body measurements of breeding eagles as described by Bortolotti (1984a, 1984b) and Garcelon et al. (1985), including hallux length, culmen length, beak depth, tarsus width, length of tail and eighth primary, and weight. A cloth tape was used to measure wing chord length across the dorsum. We compared the means for each measurement (t -test) from Arizona (10 males, 4 females), northern California (9 males, 11 females) and the Greater Yellowstone Ecosystem in Wyoming and Montana (12 males and 6 females; A. Harmata unpubl. data).

RESULTS AND DISCUSSION

Reproduction. Over the 7-year period of our study (1987–93), the occupancy rate in central Arizona was 90% (183 of 204 known territory/years) as compared to a mean of 71% for numerous other North American populations reviewed by Stalmaster (1987). Nest success in Arizona was 45%, mean brood size 1.5 young and productivity 0.69 young ($SE \pm 0.08$) per occupied site (Table 1). Except for brood size, these figures are the lowest reported in a sample of nine other populations in the coterminous U.S. for roughly the same period (Table 2).

On average, only 11.9 (range = 9–16) of the 23–30 pairs were productive in any one year (Table 1). For the most part, the low productivity resulted not from failure to lay eggs but from loss of eggs or young. These results were surprising in view of the nest protection and frequent enhancement of nestling survival by the ABENWP, active since 1978. Young blown from nests by high winds and those threatened by impending inundation or the loss of a parent were replaced or fostered into other nests (Grubb 1984).

Egg Mortality. During our 7-yr study, 73 (31%) of 237 known eggs perished or were infertile, a figure comparable to the 25% reported by Stalmaster (1987) for other North American populations. Of 24 eggs (in 13 clutches) for which we knew the mortality cause, 11 involved human disturbance, four (two clutches) were lost to nest inundation by filling reservoirs, six (three clutches) to a polygynous relationship where the male assisted only his primary mate, two when a female ceased incubating because of apparent physiological distress, and one involving an exceptionally small egg.

Seven addled eggs we collected during 1986–89 averaged 5.5 ppm DDE (range = 2.3–9.5) and 2.2

Table 1. Known productivity at Arizona bald eagle breeding areas during 1970–93.¹ Terminology follows Postupalsky (1974).

YEAR	KNOWN BREEDING AREAS	OCCUPIED NESTS	SUCCESSFUL NESTS	YOUNG FLEDGED	% NEST SUCCESS	MEAN BROOD SIZE	PRODUCTIVITY
1970	2	2	2	3	100.0	1.5	1.50
1971	3	3	3	4	100.0	1.3	1.33
1972	4	3	0	0	0.0	0.0	0.00
1973	6	5	5	7	100.0	1.4	1.40
1974	8	5	3	6	60.0	2.0	1.20
1975	9	7	4	5	57.0	1.2	0.71
1976	9	5	4	7	80.0	1.7	1.40
1977	9	7	3	6	42.9	2.0	0.86
1978	11	10	6	9	60.0	1.5	0.90
1979	12	10	4	6	40.0	1.5	0.60
1980	12	9	3	5	33.3	1.7	0.56
1981	13	10	8	16	80.0	2.0	1.60
1982	14	13	8	14	61.5	1.7	1.07
1983	15	13	7	13	53.8	1.9	1.00
1984	18	17	8	15	47.1	1.9	0.88
1985	20	19	13	22	68.4	1.7	1.16
1986	21	16	12	17	75.0	1.4	1.06
1987	26	24	11	20	45.8	1.9	0.83
1988	27	23	15	24	65.2	1.6	1.04
1989	28	25	9	13	36.0	1.4	0.52
1990	28	26	9	14	34.6	1.6	0.54
1991	29	26	13	20	50.0	1.5	0.77
1992	32	30	10	14	33.3	1.4	0.47
1993	34	29	16	22	55.2	1.4	0.76

¹ Data from 1970 through 1985 from Rubink and Podborny (1976), Hildebrandt and Ohmart (1978), Hildebrandt (1981), Ohmart and Sell (1980), Haywood and Ohmart (1980, 1981, 1982, 1983), Grubb et al. (1983), Grubb (1984, 1986).

Table 2. Productivity comparison of bald eagle populations within the coterminous United States over a similar period.

REGION	PERIOD	OCCUPIED NESTS	PERCENT NEST SUCCESSSES	MEAN BROOD SIZE	PRODUCTIVITY	SOURCE
Florida	1988	399	69	?	1.1	Wood et al. 1990
Louisiana	1988	36	67	?	1.1	Wood et al. 1990
Texas, Southeast	1981–90	193	64	1.5	0.98	Mabie et al. 1994
Colorado + Wyoming	1981–89	85	63	1.9	1.21	Kralovec et al. 1992
South Carolina	1988	50	82	?	1.4	Wood et al. 1990
Virginia	1988	84	77	?	1.4	Wood et al. 1990
Chesapeake Bay	1981–90	1448	70	1.7	1.21	Buehler et al. 1991
Maryland	1988	97	79	?	1.4	Wood et al. 1990
California	1987–93	69	58	1.6	0.90	Jackman (unpubl. data)
Arizona	1987–93	183	45	1.5	0.69	(this study)

ppm PCBs (range = 1.2–3.9) wet weight (Jenkins et al. 1994). No DDE effect on productivity was apparent in the breeding areas from which eggs were obtained, although Wiemeyer et al. (1984) reported that DDE levels of this magnitude were associated with a 50% depression of productivity in a 14-state study during 1969–79. A mean thinning rate of 6.9% for 156 eggshell fragments (including membrane) was well below the 10% level associated with reduced productivity in other bald eagle populations (Wiemeyer et al. 1984, Nisbet 1989). These findings are similar to those reported by Grubb et al. (1990) for Bald Eagles in Arizona from 1977–85.

Nestling Fatalities. During our study, 37 (22.6%) nestlings died among the 164 known to have hatched, as compared with 15% reported by Stalmaster (1987) for other populations. However, few studies were likely to have monitored nests as closely as those in Arizona where many were watched continuously throughout the breeding season. We recorded an additional six fatalities around the time of first flights from the nest. Weather-related factors were the apparent cause of death in 23 (53%) of the 43 total cases. In 1988 and 1989, heat stress appeared to be the primary agent in the death of 11 young (see Nelson 1969, Beecham and Kochert 1975, Hayes and Gessaman 1980). During 1992 and 1993, heavy rains and flood conditions were the apparent cause of 11 fatalities and the destruction of 10 nests. Additional causes of death included Mexican chicken bug (*Haematosiphon inodorus*) infestations ($N = 5$) (see also Grubb et al. 1986), falling from (or being blown out of) nests ($N = 4$), human disturbance before self-thermoregulation ($N = 3$), Great Horned Owl (*Bubo virginianus*) predation ($N = 2$), entanglement in monofilament fishing line ($N = 2$), and bacterial infections ($N = 2$).

Heavy rains not only directly caused nestling mortality, they also transformed rivers and creeks into muddy torrents, reducing fish availability (Grubb 1995). Only two of 14 breeding pairs on free-flowing river reaches successfully raised young in 1992, a flood year. We examined prey remains from the two successful nests and found significantly higher mammalian numerical composition ($\chi^2 = 18.4$, $df = 1$, $P < 0.005$ and $\chi^2 = 7.4$, $df = 1$, $P < 0.01$) compared to remains we collected during 1986–90 from these same nests.

Breeder Fatalities and Turnover. Thirteen fatalities were documented for Arizona Bald Eagle

breeders from 1951–93. Two were killed by other Bald Eagles, one by a Golden Eagle (*Aquila chrysaetos*), one by a Peregrine Falcon (*Falco peregrinus*), five were shot, one died of impact injuries, and three died of unknown causes. We infer an additional 46 breeder fatalities (24 males, 21 females, 1 unknown) from replacement of pair members (Gould and Fuller 1995). No marked breeder was seen after its replacement. The two oldest known breeders were 14 years old in 1993, with site tenures of 11 and 10 years.

Considering only the 1987–93 period, we recorded 41 fatalities or replacements during 262 monitored breeder/years. If replacements equate to fatalities, the (maximum) point estimate of breeder survival becomes 0.84 (95% C.I. = 0.78–0.88) (Trent and Rongstad 1974), a figure somewhat lower than that reported in three other studies (i.e., 0.88 by Bowman et al. (1995) in Alaska, 0.93 by Hodges et al. (1987) in Alaska and 0.93 by Gerrard et al. (1992) in Canada. Because some deaths and replacements in Arizona likely went undetected, our estimate was doubtless biased toward higher survival, as may have been the case with the estimate of Gerrard et al. (1992). The estimates for Alaska were based on samples of radio-tagged eagles.

Breeding Eagles in Subadult Plumage. Bald eagles normally defer first breeding until at least 5–8 years of age (Hansen and Hodges 1985, Buehler et al. 1991, Gerrard et al. 1992, Bowman et al. 1995). Healthy raptor populations typically contain many floaters unable to obtain breeding territories because suitable habitat is saturated by breeding pairs (Newton 1979). However, during the seven years of our study, the Arizona population appeared to contain relatively few floaters, as evidenced by a high incidence of breeding eagles displaying subadult (nondefinitive) characteristics (24 of 131 monitored pairings, 18.3%). This and the incidence of replacements by young eagles ($\geq 44\%$) were far higher than reported elsewhere (Herrick 1924, Bent 1937, Gerrard et al. 1978, Sherrod et al. 1976, Stalmaster 1987, Mabie et al. 1994, Anthony et al. 1994). In a long-term study involving thousands of Bald Eagle pairings in Saskatchewan, Gerrard et al. (1983) noted only two subadults paired with full-adults and neither pair laid eggs. Among hundreds of pairs at Chesapeake Bay, Buehler et al. (1991) observed no subadults and Hansen and Hodges (1985) remarked that subadults were not known to breed in southeastern

Alaska. Swenson et al. (1986) noted five subadults paired with full-adults in 11 years of data for 40–50 pairs in the Greater Yellowstone Ecosystem (1972–82); only two such pairs repaired a nest or laid eggs and none reproduced.

Some of the pairings and replacements in Arizona by eagles in subadult plumage may reflect a possibly atypical delay in the acquisition of full adult (definitive) plumage. J. Driscoll noted that six of 23 eagles of known age (5 females, 1 male) retained eye-stripes at greater than five years of age, and two of these still displayed eye-stripes at seven years of age. McCollough (1986) reported that two of 13 individuals in Maine retained eye-stripe remnants at six to eight years.

Pairs with members displaying subadult plumage in Arizona were more productive than those in other studies. Among the 40 pairings containing subadults at 35 occupied nests since 1970, 16 (46%) successfully fledged young, three (9%) hatched young that died in the nest, four (11%) laid eggs that did not hatch, and the remaining 12 (34%) apparently did not lay eggs. Of the five pairs with both members in subadult plumage, three apparently did not lay eggs and two hatched two young each. Although significantly more full-adult pairs laid eggs than did subadult or mixed pairs ($\chi^2 = 8.0$, $df = 1$, $P < 0.005$), we found no significant difference in nest success or productivity.

Relationship to Other Populations. There is some evidence that the Arizona Bald Eagle population may be augmented by immigration from other regions. We were able to read the bands of 14 of 29 banded breeders during 1987–93. All 14 had been banded as nestlings in Arizona. Six of the unidentified birds were banded on the left tarsus, but according to banding records, only four Arizona nestlings had been so banded. Thus, at least two breeders may have originated from outside Arizona. In 1994, an eagle banded as a nestling by Mabie et al. (1994) in southeast Texas (1410 km away) bred at a high altitude reservoir (2438 m) in the pine-forested mountains of eastern Arizona near the New Mexico border.

Arizona adults were, on average, smaller in all morphological characteristics than those from Alaska, California, or the Greater Yellowstone region, a finding that supports an affinity of the Arizona population with those in the southeastern U.S. as proposed by Amadon (1983), Stalmaster (1987), and Palmer (1988). Arizona males were significantly smaller in 13 of 16 measurements (Table

3) and females in eight of 16 comparisons, a difference probably arising from the small number of females sampled. Morphological measurements of two adults from the Rio Yaqui, Sonora, Mexico did not differ from those in Arizona.

These results suggested that the Bald Eagle population in the southwest either rebounded from a depleted population or derived from immigration from the southeastern U.S., or both. If gene flow into Arizona from north or west (where eagles are larger) had recently occurred, it should at least be reflected in the overall variance of mensural characters, assuming that the environmental component of such variation is weak compared with the genetic component. We examined this hypothesis by comparing coefficients of variation for the various characters we measured in the four populations, but found no suggestion of greater variance within the Arizona sample.

SUMMARY OF STATUS

Despite the uncertainty of determining whether newly discovered pairs equate to newly occupied territories, the weight of evidence indicates a continuing upward trend in the number of Bald Eagle pairs in Arizona since 1970. This trend is occurring with little direct evidence of augmentation by immigrants and despite relatively low estimates of productivity and breeder survival. The substantial incidence of pairs containing members in subadult plumage suggests a deficient age structure in the floating segment and thus a relatively small recruitment buffer (Hunt 1998). A paucity of floaters may, in part, result from continued population expansion (i.e., eagles that would otherwise become floaters are founding new territories). However, we do not discount the role of low vital rates (e.g., breeder survival) in retarding floater accrual. We therefore recommend monitoring of breeding sites and continuation of population-wide VID banding. Because of the proven benefit of the ABENWP in enhancing reproduction, we recommend its continuance at sites where human disturbance is considered significant.

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Table 3. Means and standard deviations for selected measurements (mm) and weights (kg) of adult male Bald Eagles from Arizona, northern California, Alaska (data from T. Bowman and P. Schempf), and the Greater Yellowstone Ecosystem (Wyoming and Montana, data from A. Harmata).

MEASUREMENT	ARIZONA	CALIFORNIA	ALASKA	YELLOWSTONE
Hallux (arc)	37.4 ± 1.3 (N = 10)	40.4 ± 0.4 (N = 7)***	41.3 ± 1.1 (N = 33)***	41.0 ± 1.5 (N = 7)***
Tarsus width (lateral)	12.4 ± 0.6 (N = 9)	13.0 ± 0.5 (N = 9)*	13.2 ± 0.6 (N = 33)**	13.8 ± 0.8 (N = 12)***
Tail length	237.0 ± 19.6 (N = 8)	265.1 ± 10.1 (N = 9)**	278.8 ± 18.1 (N = 33)***	273.0 ± 9.2 (N = 8)***
Culmen (arc)	48.3 ± 1.1 (N = 10)	52.4 ± 1.1 (N = 9)***	52.4 ± 1.7 (N = 33)***	51.3 ± 1.4 (N = 12)*****
Weight	3.3 ± 0.2 (N = 12)	4.1 ± 0.3 (N = 10)***	4.7 ± 0.3 (N = 32)***	4.1 ± 0.3 (N = 10)***

Comparisons (ttest) with Arizona samples: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

access to remote breeding areas for nest climbs. We thank M. Greenburg and T. Noble (SRP) and C. Thelander (BioSystems Analysis, Inc., BSAI) and numerous BSAI employees for their assistance during our study. We acknowledge the work of D. Rubink (USFWS), R. Ohmart, T. Hildebrandt, D. Haywood and R. Sell (Arizona State University), T. Grubb, W. Eakle and L. Forbis (USFS), and the hundreds of ABENWP personnel who have watched over Arizona's nesting eagles since 1978. We acknowledge D. Bland, L. Kiff, and R. Risebrough for work concerning eggshell thinning and contaminants. We thank J. Linthicum, T. Hunt, and two anonymous reviewers for valuable comments on the manuscript.

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THE INFLUENCE OF WEAPONS-TESTING NOISE ON BALD EAGLE BEHAVIOR

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ABSTRACT.—We studied the influence of weapons-testing noise on Bald Eagle (*Haliaeetus leucocephalus*) behavior at the Aberdeen Proving Ground (APG), Maryland, in 1995. Our objectives were to document and compare eagle behavior at times with and without weapons-testing noise, determine if the frequency of behavior after noise increased with increasing sound levels and compare nest success and productivity on APG with that of adjacent areas of Maryland. Most roosting (72.7%) and nesting (92.7%) eagles showed no activity (i.e., perched motionless) in the 2-sec interval following weapons-testing noise. The most frequent activity following noise was a head turn, exhibited by 18.2% of roosting and 0.7% of nesting eagles; other eagle activities following noise (e.g., body movement, vocalization and flight) were rare at both roosts (9.1%) and nests (6.6%). Frequency of activity after noise differed between adults and juveniles at nests, but did not differ between adults and immatures at roosts. Activity after noise occurred significantly more in roosting than nesting eagles. For roosting eagles, frequency of activity after noise was similar to activity at times without noise. Frequency of no activity versus activity after noise did not vary at sound intensity levels ≥ 110 and < 110 dBP for either nesting or roosting eagles. Nest success and productivity on APG did not differ from nest success and productivity in adjacent counties of Maryland from 1990–95, suggesting that weapons-testing noise did not influence eagle reproduction at the population level.

KEY WORDS: *Bald Eagle*, *Haliaeetus leucocephalus*; *behavior*, *Chesapeake Bay*, *human disturbance*, *Maryland*; *noise effects*.

Influencia del ruido de prueba de armas en el comportamiento de águilas calvas

RESUMEN.—Estudiamos la influencia del ruido de la prueba de armas en el comportamiento de las águilas calvas (*Haliaeetus leucocephalus*) en el Campo de Pruebas de Aberdeen (CPA), Maryland en 1995. Nuestros objetivos fueron los de comparar el comportamiento de las águilas con y sin ruidos de prueba de armas, determinar si la frecuencia de comportamiento después del ruido aumenta con los niveles de sonido y comparar el éxito de anidación y productividad en el CPA y en áreas adyacentes de Maryland. Las águilas en perchas (72.7%) y en anidación (92.7%) no mostraron ninguna actividad en el intervalo de 2 segundos después de la prueba de armas. La actividad mas frecuente después del ruido

fue la de girar la cabeza, exhibida por el 18.2% de las águilas en perchas y 0.7% de las águilas en anidación. Otras actividades después del ruido (movimientos de cuerpo, vocalizaciones y vuelo) fueron raras en las águilas en perchas (9.1%) y en nidos (6.6%). La frecuencia de actividad después del ruido difirió entre adultos y juveniles en los nidos, pero no entre adultos y juveniles en perchas. La actividad fue significativamente mayor en las águilas en perchas que en anidación. Para las águilas en perchas la frecuencia de actividad después del ruido fue similar a la de actividad sin ruido. La frecuencia de respuesta de inactividad versus actividad después del ruido no varió con la intensidad del sonido 110 y 110 dBP tanto para las águilas en anidación o en perchas. El éxito de anidación y productividad en el CPA no difirió del éxito de anidación y productividad de los condados adyacentes de Maryland entre 1990–95, lo cual sugiere que el ruido de la prueba de armas no afecta la reproducción de las águilas a nivel poblacional.

[Traducción de César Márquez]

Despite studies directly or indirectly addressing the influence of unnatural sound energy, hereafter referred to as noise, from military activities on raptors (e.g., Andersen et al. 1986, Mancini et al. 1988, Andersen et al. 1989, Stalmaster and Kaiser 1997), there is little consensus on the overall influence of noise on them. Nine of 17 Red-tailed Hawks (*Buteo jamaicensis*), not previously exposed to helicopter overflights, flushed from nests exposed to helicopter activity (Andersen et al. 1989), although noise and visual parameters of helicopter disturbance were not examined separately. Grubb et al. (1992) reported noise from artillery fire located a median distance of 1.5 km from nesting Bald Eagles (*Haliaeetus leucocephalus*) elicited no visible behavioral response in 100% of 25 eagle-noise observations. Stalmaster and Kaiser (1997) reported that 8% of 1452 Bald Eagles flushed during 373 weapons-firing events on the Fort Lewis Army Reservation, Washington. The influence of weapons-testing noise on raptor behavior or reproductive fitness has not been quantitatively examined in other studies, and decibel levels associated with raptor behavior following weapons-testing noise have not previously been documented. Because military installations comprise approximately 9.7 million ha in the U.S. (Pfister 1988), applied information on the effects of weapons-testing noise could be useful in developing raptor management guidelines for military installations.

We studied the influence of noise from military weapons-testing at the Aberdeen Proving Ground (APG), Maryland, on nesting and roosting Bald Eagle behavior, nest success, and productivity. Our objectives were to document eagle behavior following weapons-testing noise, determine if frequencies of behavior after noise differed by age, test the null hypothesis that roosting eagle behavior after noise did not differ from behavior at times without

noise, test the null hypothesis that the frequency of active behaviors after noise did not increase with increasing sound levels and compare nest success and productivity on APG with that of adjacent areas of Maryland. In addition to using nest success and productivity on APG as an indirect measure of the influence of weapons-testing noise, this comparison served as a relative indicator of habitat quality. The study area was an ideal locale to examine the influence of noise on eagle behavior because of the abundance of eagle nests and roosts (Buehler et al. 1991a, 1991b) and because of high levels of weapons-testing noise prior to and during our study.

METHODS

APG is a 350 km² military installation located on the western shore of the northern Chesapeake Bay, 30 km north of Baltimore, Maryland. Access to much of APG is restricted, greatly reducing human-associated activities that may negatively influence eagle behavior and distribution (Buehler et al. 1991c, Chandler et al. 1995). The area is dominated by forests of various ages except for the developed Aberdeen and Edgewood cantonment areas and scattered test ranges with open fields. Most of APG is at or near sea level with a largely undeveloped shoreline characterized by marshes and forested wetlands. Testing of ordnance and weapons has been the primary mission of APG since 1917. Up to several thousand impulsive (<1 sec) noise events/day may occur at various test ranges across the installation as a result of explosive detonations and small arms, tank and artillery fire (U.S. Army 1994). Weapons-testing noise rarely occurs at night.

Observations on eagle behavior after weapons-testing noise were gathered at three nests (11 total individuals sampled) in May and June 1995; observations on roosting eagle behavior after noise events were made throughout 1995 at two large communal roosts (≤ 58 eagles/roost). Monthly aerial surveys from 1993–95 located up to 94 nesting and roosting eagles on APG. Eagles were not banded or marked, and we were unable to differentiate between most eagles of similar age. Therefore, we were not able to determine the extent of pseudoreplication in roosting eagles, but estimated it to be very low due to

large daily variance in eagle abundance at roosts (Buehler et al. 1991b) and seasonal turnover in roosting populations due to migration (Buehler et al. 1991a). Levels of prior exposure to weapons-testing noise was unknown for individual eagles.

All nests and roosts were at least 0.5–4 km from test ranges and typically experienced noise events from more than one range. No ranges were visible from nests or roosts due to intervening forests. All noise events resulted from scheduled weapons-testing activities and none were staged for the purpose of this study. Nest observations were made throughout the day and roost observations were made from about 1.5 hr before sunset until dark. Observers used 15–45× spotting scopes from either a fixed blind or stationary vehicle. A 1–60× video camera was used to record and later review some eagle behavior after noise. Eagle ages were classified as adult (white head and tail), immature (mottled or all-dark plumage), or juvenile (nestling) (Bortolotti 1984).

Eagle behavior was recorded in an arbitrary 2-sec interval immediately following each weapons-testing noise event. A 2-sec interval was chosen because our preliminary evaluations of eagle behavior following noise events suggested this was an appropriate interval to detect noise-related behaviors, if any, and because intervals >2 sec had an increasing probability of detecting behaviors unrelated to noise. Behaviors were categorized as follows: 0 = no discernible activity (i.e., perched motionless); 1 = head turn; 2 = body or wing movement; 3 = vocalize; 4 = take to flight; 5 = preen; and 6 = other. We assumed that categories 0–4 described increasing energetic levels of activity; categories 5–6 represented miscellaneous behaviors. A head turn toward the source of an auditory stimulus is known as an orienting response (Brown 1990). However, head turns recorded in our study included those toward the noise source, away from the noise source and up.

We did not attempt to classify eagle behavior as a response or no response to noise because of inherent subjective assumptions involving cause and effect and because all behaviors we classified were within eagles' normal behavioral repertoire and could have occurred at any time, regardless of noise. Sample sizes of ≥ 1 often resulted from single noise events if several eagles were under observation. Eagles exposed to occurrences that could have influenced their behavior after noise (e.g., interactions with other eagles) were eliminated from analysis.

We collected control data to test the null hypothesis that no difference existed between roosting eagle behavior after noise compared to times without noise, using the seven previous categories. Control roosting behavior was collected in 30 consecutive 2-sec intervals/0.5 hr beginning about 1.5 hr before sunset and continuing until dark from January–December 1995 on the same days and at the same roosts that experimental roosting behavior was being gathered.

Levels of weapons-testing noise were measured in unweighted peak decibels (dBP) using a Larson Davis Laboratories 870 precision integrating sound level analyzer, a Larson Davis 2100 preamplifier and a Larson Davis 2541 microphone. Sound level analyzers were calibrated using either a Bruel and Kjaer 4230 sound level calibrator

or a Metrosonics CL304 acoustic calibrator. Microphones were located 3.0 m above ground and within approximately 100 m of nests and roosts. Inaccuracies in dBP levels due to the distance between microphones and eagles were estimated to be <1 dBP based on the nature of impulsive sound energy and the dBP scale, the relatively large distances (≥ 0.5 km) from firing range to microphone and the standard acoustical formula for determining sound level differences between two receiving locations (Harris 1979). Observers synchronized their watches to the nearest sec with sound level analyzers so behavioral observations could be paired with corresponding noise events. Some dBP data were gathered using a Larson Davis portable sound level analyzer 800B (type I), a Larson Davis 826B pre-amplifier and a Larson Davis 2559 microphone; the sound level analyzer was calibrated before and after use with a Metrosonics CL304 calibrator.

We monitored eagle nest success and productivity on APG (experimental) versus adjacent areas (control) from 1990–95 to indirectly evaluate the possibility that weapons-testing noise influenced eagle reproduction on APG by affecting nest abandonment and failure. Nest sites were aerially monitored during three visits/season from February through May to determine occupancy and fate. We analyzed four measures of eagle reproduction: nest success (% of successful nests/occupied territory) and productivity (number of young assumed fledged/occupied territory, young assumed fledged/breeding pair and young assumed fledged/successful nest [Postupalsky 1974, Steenhof 1987]). Adjacent areas of Maryland included Baltimore, Cecil, Harford and Kent counties.

Behavior categories 1–6 were combined and compared to category 0 in all statistical tests because categories 2–6 were rarely observed. Thus, all behavior comparisons evaluated the difference between frequencies of no discernible activity versus some activity. Chi-square tests for association were used in all behavioral comparisons and in comparison of nest success. Mean nesting productivity on APG versus adjacent counties from 1990–95, was compared using independent sample *t*-tests with SPSS software (Norusis 1993). Statistical significance was accepted at $P \leq 0.05$.

RESULTS

The most common eagle behavior in the 2-sec interval following weapons-testing noise at nests and roosts was no activity, recorded after 92.7% and 72.7% of noise events, respectively (Table 1). The most frequent activity after noise at nests and roosts was a head turn, recorded after 0.7% and 18.2% of noise events, respectively. Other activity categories (2–6) were recorded for 6.6% and 9.1% of eagle behavior after noise at nests and roosts, respectively.

Nesting adults and juveniles showed activity after noise in 1 (1.8%) of 55 and 10 (10.4%) of 96 observations, respectively. Roosting adults and immatures exhibited activity after noise in 8 (25%) of 32 and 28 (28%) of 100 observations, respec-

Table 1. Nesting and roosting Bald Eagle behavior in the 2-sec interval following weapons-testing noise (experimental) and at times without noise (control), Aberdeen Proving Ground, Maryland, 1995. Behavior categories included: 0 = no discernible activity; 1 = head turn; 2 = body or wing movement; 3 = vocalize; 4 = take to flight; 5 = preen; and 6 = other.

EAGLE LOCATION	NOISE STATUS	NUMBER OF EAGLE BEHAVIORS BY CATEGORY							TOTAL
		0	1	2	3	4	5	6	
Nest	Experimental	140	1	0	0	0	10	0	151
Nest	Control	None gathered							
Roost	Experimental	96	24	2	4	0	6	0	132
Roost	Control	5596	1201	76	72	15	1038	229	8227

tively. Frequencies of no activity compared to activity behavior categories after noise differed between adults and juveniles at nests ($\chi^2 = 3.82$, $df = 1$, $P = 0.05$), but did not differ between adults and immatures at roosts ($\chi^2 = 0.11$, $df = 1$, $P = 0.74$), although our study was not designed to test for differences between age classes. Therefore, all age classes were combined for subsequent analyses. The frequency of active behaviors following noise was higher for roosting eagles than for nesting eagles ($\chi^2 = 20.32$, $df = 1$, $P < 0.001$).

The most frequent behavior recorded for roosting eagles at times without weapons-testing noise was no activity, accounting for 68.7% of control observations (Table 1). Frequencies of no activity versus activity categories did not differ between control and experimental roost observations ($\chi^2 = 1.28$, $df = 1$, $P = 0.26$). Because it appeared unlikely that preening and other behavior (categories 5 and 6, respectively) were reactions to noise events, we compared control and experimental roosting data in two additional ways: without inclu-

sion of these two categories and including these categories as no activity. We could not detect a difference between control and experimental behavior at roosts ($\chi^2 = 3.12$, $df = 1$, $P = 0.08$ and $\chi^2 = 1.27$, $df = 1$, $P = 0.26$, respectively) in either comparison.

Despite a lack of difference between experimental and control roost behavior, a small number of activity behaviors following ordnance noise appeared to be a direct result of noise. For example, a roosting immature eagle that was preening appeared to lose its balance and nearly fell off its perch immediately after an explosion measuring 120.1 dBP on 11 September. However, we did not observe any eagles taking to flight immediately after noise during the study period, although we observed this activity once after noise during a 1994 preliminary study.

Behavioral observations at nests and roosts following weapons-testing noise were paired with dBP levels ranging from 82–126 dBP (Table 2). We recorded dBP data for all observations at nests but for only 58% of observations at roosts because of wind interference and equipment malfunction. Because of small sample sizes for some dBP levels and because we had no reason to divide dBP categories at any particular level for analysis, we chose to compare frequencies of activity after noise between <110 dBP and ≥ 110 dBP. The 110 dBP threshold was chosen to attempt to obtain approximately equal sample sizes for roosts and nests. We did not detect a difference in frequencies of no activity versus activity at sound levels ≥ 110 than at <110 dBP for nesting ($\chi^2 = 3.01$, $df = 1$, $P = 0.08$) and roosting eagles ($\chi^2 = 2.94$, $df = 1$, $P = 0.09$).

Overall nest success did not differ for 1990–95 between APG (61 occupied territories, 41 successful nests, 67% nest success) and adjacent areas of

Table 2. Nesting and roosting Bald Eagle behavior in the 2-sec interval following weapons-testing noise by decibel (dBP) level, Aberdeen Proving Ground, Maryland, 1995. Behavior categories have been summarized into no activity (category 0) and activity (categories 1–6).

dBP LEVELS	NUMBER OF EAGLE BEHAVIORS BY CATEGORY					
	NESTING EAGLES			ROOSTING EAGLES		
	0	1–6	TOTAL	0	1–6	TOTAL
80–89	—	—	—	1	1	2
90–99	—	—	—	—	—	—
100–109	52	7	59	32	21	53
110–119	68	2	70	2	3	5
120–129	20	2	22	6	10	16

Table 3. Summary measures of Bald Eagle reproduction ($N = 209$ occupied territories) on Aberdeen Proving Ground (APG) compared to adjacent areas (ADJ) along the northern Chesapeake Bay, Maryland, 1990–95. Test statistics are from analyses to determine if differences existed between APG and ADJ for 1990–95.

PARAMETERS STATISTICS	SUMMARY DATA			TEST		
	STATISTIC	APG	ADJ	t	df	P
Young fledged/occupied territory	N	61	148			
	mean \pm SD	1.13 ± 0.90	1.09 ± 0.96	0.26	207	0.80
Young fledged/breeding pair	N	59	136			
	mean \pm SD	1.17 ± 0.89	1.19 ± 0.94	−0.15	193	0.88
Young fledged/successful nest	N	41	96			
	mean \pm SD	1.68 ± 0.52	1.69 ± 0.64	−0.04	135	0.97

Maryland (148 occupied territories, 96 successful nests, 65% nest success; $\chi^2 = 0.11$, $df = 1$, $P = 0.75$). Overall numbers of young/occupied territory, young/breeding pair, and young/successful nest for 1990–95 combined were not significantly different on APG compared to adjacent areas of Maryland (Table 3).

DISCUSSION

Behaviors that were likely indications of severe noise disturbance, such as body or wing movement and flight, occurred infrequently or were absent during both control and experimental observations. Although some eagles apparently reacted, our findings suggest that most eagles have habituated to weapons-testing noise. We did not demonstrate that habituation has occurred, but our findings were consistent with a habituation hypothesis. Habituation is an active learning process that permits individuals to discard a response to a recurring stimulus for which constant response is biologically inappropriate without impairment of their ability to respond to other stimuli (Lorenz 1965, Alcock 1979, Peeke and Petrinovich 1984). Because this constitutes tolerance for prolonged and repetitive activities, then the thousands of noise events caused by weapons testing on a typical day at APG would be a likely basis for habituation. Habituation could occur in a relatively short time even for nonresident eagles that migrate into the area. Apparent habituation by many vertebrates to similar noise has been widely documented (e.g., Andersen et al. 1989, Grubb and King 1991, Weisenberger et al. 1996). Perhaps most unexpected was our finding of apparent eagle habituation to most weapons-testing noise exceeding 120 dBP. For comparison, naturally-occurring thunder ranges

from 82–103 dBP at distances of 700–2100 m (Holmes et al. 1971).

An alternative hypothesis is that some eagles reacted to weapons-testing noise by more frequently ceasing activity (i.e., they “froze”). For example, a decrease in flight activity was reported in cave-roosting bats exposed to noise from low-level supersonic aircraft overflights at Organ Pipe Cactus National Monument in Arizona (V.M. and D.C. Dalton unpubl. data). However, we did not address this hypothesis, which would require evaluating behavior immediately before and after noise.

The null hypothesis that eagle activity after noise did not increase with increasing sound level was not rejected. Sensitization, defined as successively stronger responses to specific stimuli (Peeke and Petrinovich 1984), apparently did not occur in eagles exposed to weapons-testing noise at APG.

Based on our finding that most eagles exhibited no activity following relatively loud noise events, we concluded that Bald Eagles at nests and roosts at APG do not show a significant behavioral reaction to weapons-testing noise. This conclusion is supported by the finding that sensitization to noise was apparently not occurring. Our finding that eagle nest success and productivity from 1990–95 was similar for APG and adjacent areas of Maryland suggests that weapons-testing noise did not influence overall reproductive performance of the nesting eagle population at APG.

Loud noise can induce stress in some animals, resulting in physiological changes such as increased heart and respiratory rates, altered blood chemistry and hormone production, hypertension and vasoconstriction (Manci et al. 1988). For example, Weisenberger et al. (1996) reported that heart rates of ungulates increased relative to in-

creasing noise levels produced by simulated jet aircraft overflights but returned to pre-disturbance conditions in 60–180 sec. Our study addressed visible behavior only, and no existing studies of the influence of noise have examined raptor physiology. We recommend that future research on the effects of noise on Bald Eagles or other raptors should focus primarily on physiology and should attempt to test for a quantitative link between noise, physiology and reproductive fitness.

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EFFECTS OF RECREATIONAL TRAILS ON WINTERING DIURNAL RAPTORS ALONG RIPARIAN CORRIDORS IN A COLORADO GRASSLAND

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ABSTRACT.—Different types of human activity may influence raptors in various ways, potentially affecting their abundance, distribution, habitat use and productivity. We studied the effects of recreational trails on wintering raptor populations in grasslands of eastern Boulder County, Colorado, from December 1995–March 1996. We conducted strip transects to survey raptor populations at six study sites. All sites consisted of short and/or tallgrass prairie, and all contained a riparian corridor. Three sites contained recreational trails running adjacent to the riparian corridor (trail), while three sites contained no trails (control). Species richness, abundance and perch use were compared between control and trail sites. Species richness was consistently greater in control sites. Abundance of total raptors observed was greater in control sites. Abundance of Bald Eagles (*Haliaeetus leucocephalus*) was greater in control sites, while abundance of Red-tailed Hawks (*Buteo jamaicensis*) was similar for control and trail sites. Perching distances from riparian corridors were greater in trail sites than in control sites. In addition, raptors perched along riparian corridors more frequently in control sites. Results of this study suggest that recreational trails may have affected habitat selection of some raptor species in this grassland ecosystem.

KEY WORDS: *raptors; human activity; recreational trails; perch use; riparian corridors; grasslands.*

Corredores ribereños en un pastizal de Colorado

RESUMEN.—Diferentes tipos de actividad humana pueden influenciar a las aves rapaces de varias maneras; potencialmente afectando su abundancia, distribución, uso de habitat, y productividad. Estudiamos los efectos de los senderos recreativos en las poblaciones de aves rapaces del este del Condado de Boulder, Colorado desde Diciembre 1995–Marzo 1996. Efectuamos transectos lineares para documentar las poblaciones de aves rapaces en seis áreas de estudio. Los sitios de estudio fueron en pastizales cortos y/o altos que contenían un corredor ribereño (sendero), mientras que tres sitios no contenían ningún sendero (control). La riqueza de especies, abundancia, utilización de perchas fueron comparadas entre el control y los sitios con senderos. La riqueza de especies fue consistentemente mayor en los sitios de control. La abundancia total de aves rapaces observadas fue mayor en los sitios de control. La abundancia de águilas calvas (*Haliaeetus leucocephalus*) fue mayor en los sitios de control, mientras que la abundancia de *Buteo jamaicensis* fue similar para ambos sitios. La distancia entre perchas de los corredores ribereños fue mayor en los sitios con senderos que en los sitios de control. Adicionalmente, las aves rapaces utilizaron con mas frecuencia las perchas a lo largo de los corredores ribereños en los sitios de control. Los resultados de este estudio sugieren que los senderos recreativos pudieron haber afectado la selección de habitat de algunas especies de aves rapaces en este ecosistema de pastizales.

[Traducción de César Márquez]

Raptor abundance and distribution can be affected by many factors, including prey availability (Howard and Wolfe 1976, Preston and Beane 1996, Gietzen et al. 1997, Plumpton and Andersen 1998), vegetation (Wakeley 1978), and the availability of

perch sites (Stahlecker 1978, Jones 1989, Janes 1994, Widen 1994). While open space areas and green belts provide potential habitats for grassland raptors in urban environments (Cringan and Horak 1989), such areas are also characterized by a variety of human activities. These human activities may affect raptor habitat use and may influence raptor abundance.

Certain effects of human activity on raptor pop-

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ulations have been extensively studied, yet with equivocal results. For example, Stalmaster and Newman (1978) found that Bald Eagles (*Haliaeetus leucocephalus*) avoid areas of high human activity. Smallwood et al. (1996) also observed many species of raptors avoiding human settlements. However, other research suggests that human activity may not affect raptor distribution and productivity (Mathisen 1968, Grier 1969, Preston and Beane 1996). Human activity may affect raptors in different ways, and some types of human activity may affect raptors more than others (Preston and Beane 1996). For instance, Fraser et al. (1985) found that nesting success of Bald Eagles was not affected by human activity; however, eagles did choose nest sites far from human development. Both Skagen (1980) and Holmes et al. (1993) found that raptors were more sensitive to humans approaching on foot than to humans approaching in vehicles.

We studied the potential effects of recreational trails on wintering grassland raptor populations in Boulder County, Colorado, during the winter of 1995–96. We compared species richness, abundance, and perch use along riparian corridors in areas with trails adjacent to corridors and areas without trails. We also compared distances between raptor perches and riparian corridors in areas with and without trails along corridors.

STUDY AREA AND METHODS

We studied raptors in the grasslands of east Boulder County, Colorado (40°00'N, 105°20'W) from December 1995 until March 1996. We chose six study sites of similar habitat on the City of Boulder Open Space property. All study sites contained riparian corridors, with adjacent vegetation consisting of short and/or tallgrass prairie. Previous research in this region showed a high correlation of raptor abundance to perch sites (Jones 1989). We chose sites containing riparian corridors with numerous potential perches to control for perch availability. All sites also contained many perches outside the riparian area, at a wide range of distances from the corridor (0–440 m). Three sites included recreational trails running adjacent to the riparian corridor (trail sites), within 15 m of the corridor at all locations. Three sites had no trails (control sites). Recreational trails were 2–3 m in width and composed of gravel. Throughout the study period, trails were used frequently each day by hikers and/or bicyclists, but were closed to vehicle use. Study site size was determined by open space boundaries, and was estimated using 7.5 min U.S. Geological Survey topographic quadrangle maps. Overall, trail sites included 72 ha ($\bar{x} = 23.9 \pm 6.1$, \pm SE) of grassland and riparian habitat, and control sites included 54 ha ($\bar{x} = 18.0 \pm 5.1$). Predominant vegetation along riparian areas included cottonwoods (*Populus sargentii*), willows (*Salix* spp.) and Russian olives (*Elaeagnus angustifolia*).

Potential prey items for raptors included lagomorphs (*Sylvilagus* spp. and *Lepus* spp.), black-tailed prairie dogs (*Cynomys ludovicianus*), and other small rodents (e.g., *Microtus ochrogaster*). None of the sites contained prairie dog colonies, but colonies were potentially within the home ranges of raptors seen on each of our study sites. We estimated the distance from the center of each site to the edge of the closest prairie dog colony, based on 1997 Boulder County Open Space digitized maps. The average distance to prairie dog colonies for control sites (2.3 ± 0.6 km) and trail sites (1.9 ± 0.3 km) did not differ statistically (two-tailed, two sample *t*-test; $t = 0.61$, $df = 4$, $P = 0.58$).

We conducted strip transects to survey raptor populations twice a week at each site from 0700–1130 H (MST). Each transect was 350 m long, parallel to the riparian corridor, at distances of 5–30 m from each corridor. Transect width was delineated based on public land boundaries, ranging from 315–450 m. For each survey, a single observer walked slowly along the transect for 15 min, recording the species and number of raptors observed within the study site, the type of perch used by perching raptors, and mapping perches used by raptors. Perch distances (i.e., distance from the perch used to the edge of the riparian corridor) were later measured when raptors were not present. We rotated the order of sites surveyed each day to control for survey time differences. We did not conduct surveys during inclement weather (e.g., snowstorms) because inclement weather could affect the detectability of raptors and there was probably less recreational activity during inclement weather. We conducted a total of 77 surveys, ranging from 10–15 for each site. We conducted 41 surveys at trail sites and 36 surveys at control sites.

We sampled vegetation along the riparian corridors and in surrounding grassland vegetation at each site. To sample riparian corridors, we walked one 300 m transect running along the grassland/riparian edge at each site, recording the species and diameter breast height (dbh) of the closest tree in each cardinal direction at 50 m intervals ($N = 24$ for each site). For sampling grassland characteristics at each site, we walked four 300 m transects running parallel to each riparian corridor at distances of 50, 100, 150, and 200 m from the edge of the corridor. Every 50 m we recorded the coarse defining characteristic of the vegetation (shortgrass prairie, tallgrass prairie, broad-leaf shrub, tree, bare ground) and visually estimated the percent ground vegetation cover within a 1 m² radius aluminum ring placed on the ground ($N = 24$ for each site).

Riparian corridors provided a high, uniform density of potential perches at each of the six sites. We quantified surrounding perch density (i.e., not including the riparian perch density) for each site by counting the total number of natural perches (i.e., trees, shrubs and snags) ≥ 2 m in height (Janes 1985) at each study site, and dividing this total by the area of the site (in ha). We did not include perch types other than trees and shrubs (e.g., utility poles), because we only observed raptors using trees and shrubs for perching in our study sites.

To directly compare surveys conducted in study sites of differing size, we analyzed the abundance of raptors as the number of raptors observed per km² surveyed, and

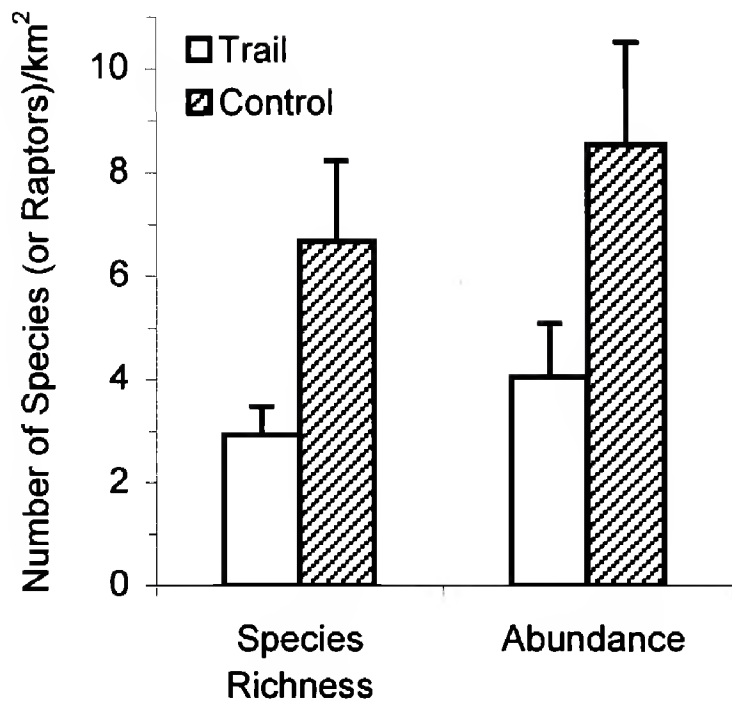


Figure 1. The total abundance and species richness ($\bar{x} \pm SE$) of all raptors observed, December 1995–March 1996. Abundance is defined as the number of raptors observed per km² surveyed. Species richness is defined as the number of species observed per km² surveyed.

species richness as the number of species observed per km² surveyed. Both species richness and abundance indices were analyzed using two-way analysis of variance (ANOVA) with a repeated measures design, using transect type (trail or control) as one factor and sampling date as the repeated measure. Using sampling date as a repeated measure allowed us to investigate any potential temporal differences in abundance and species richness within the sampling period. We used the procedure, PROC MIXED on SAS statistical software, to run the repeated measure ANOVA analyses, because this procedure can accommodate unbalanced repeated measure designs (SAS 1997).

The data collected for perching distances from riparian corridors were not normally distributed and therefore were analyzed using a Kruskal-Wallis nonparametric test (with Chi-square approximation, SAS 1989). We investigated potential temporal differences in perching distance from corridors by regressing the response variable, perching distance, on sampling date (PROC GLM, SAS 1989). The frequency of use of riparian areas for perching was analyzed using a χ^2 contingency table, with transect type (trail or control) as one criterion, and number of perching events on and off riparian areas as a second criterion.

We analyzed dbh, percent ground cover, and perch availability for trail and control sites using one way ANOVAs. Species composition of the riparian canopy was analyzed using a χ^2 goodness-of-fit test against the null expectation of equal numbers of trees in trail and control sites. For all analyses, we chose $\alpha = 0.05$. Arithmetic means $\pm SE$ are reported.

RESULTS

Species Composition. Seven species of raptors were observed during our study, including (in de-

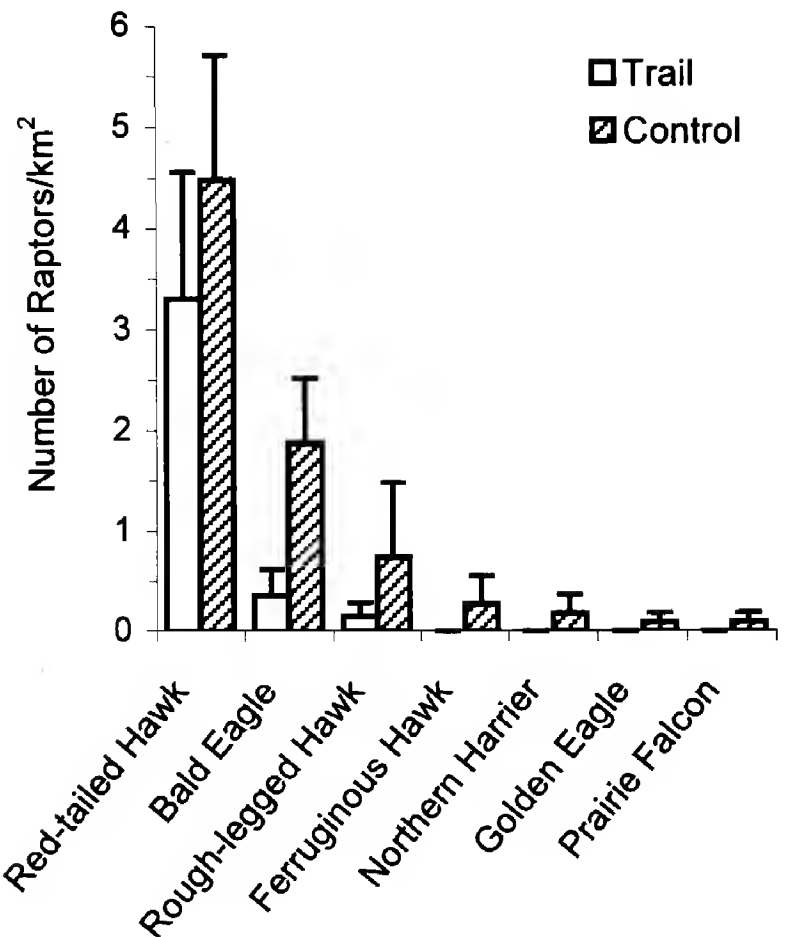


Figure 2. Abundance indices ($\bar{x} \pm SE$) of each species observed at trail and control sites, December 1995–March 1996. Abundance is defined as the number of raptors observed per km² surveyed.

creasing frequency of observation): Red-tailed Hawks (*Buteo jamaicensis*), Bald Eagles, Rough-legged Hawks (*Buteo lagopus*), Ferruginous Hawks (*Buteo regalis*), Northern Harriers (*Circus cyaneus*), Golden Eagles (*Aquila chrysaetos*) and Prairie Falcons (*Falco mexicanus*). Seven species were observed in control sites, while only three were observed in trail sites. We observed a consistent pattern of greater species richness in control sites (ANOVA: $F = 12.67$, $df = 1$, $P < 0.001$) (Fig. 1).

Raptor Abundance. Abundance indices for total raptors were greater at control sites (ANOVA: $F = 9.70$, $df = 1$, $P = 0.003$) (Fig. 1). Abundance indices for Red-tailed Hawks were similar for control and trail sites (ANOVA: $F = 1.52$, $df = 1$, $P = 0.224$) (Fig. 2). Bald Eagle abundance indices were greater in control sites (ANOVA: $F = 6.25$, $df = 1$, $P = 0.016$). We pooled all other species of raptors, due to small sample size. Abundance indices for these raptors were greater in control sites (ANOVA: $F = 7.29$, $df = 1$, $P = 0.010$). For all abundance and species richness analyses, sampling date as the repeated measure was not significant ($P \geq 0.15$), and there were no statistically significant interactions among the two factors ($P \geq 0.3$), suggesting

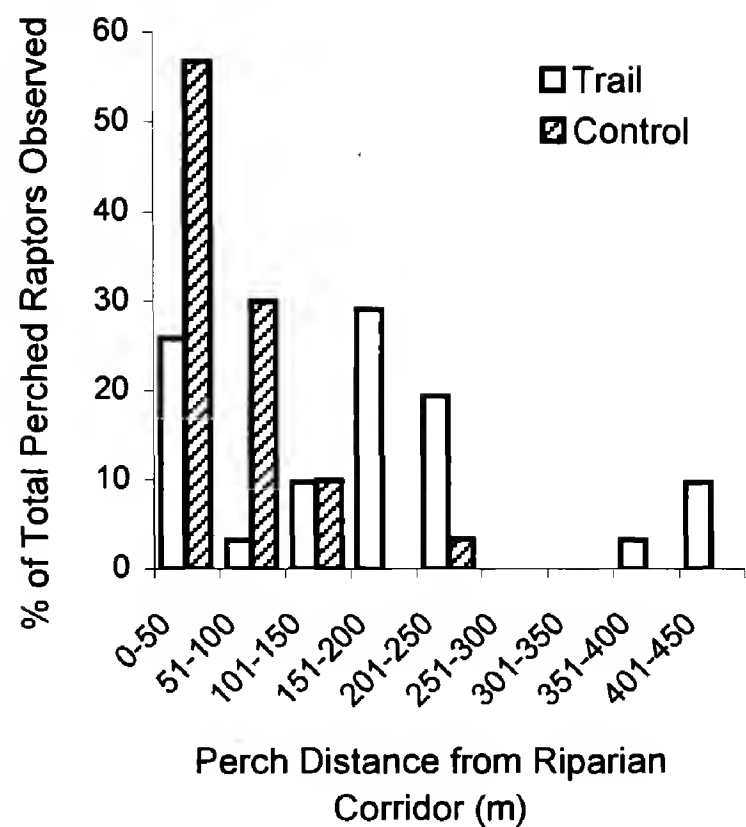


Figure 3. The distribution of raptor perching distances from riparian corridors in trail and control sites, December 1995–March 1996. Perch distance was measured from the perch used to the riparian corridor (m).

both the abundance and species richness of raptors did not change temporally during the sampling period.

Perch Use. During the study period, 60.2% ($N = 56$) of all raptors were observed perching. In all observations, raptors used deciduous trees and snags for perching, even though fence posts, power lines and utility poles were present at the study sites. The distribution of perching distances from riparian corridors was different in control and experimental sites (Fig. 3), where the mean perch distance from riparian corridors was significantly greater in trail sites (155.9 ± 28.0 m) than in control sites (42.3 ± 9.8 m) (Kruskal-Wallis: $\chi^2 = 18.97$, $df = 1$, $P < 0.001$). In addition, raptors perched along riparian corridors significantly more often in control sites (54.8%, $N = 17$) than in trail sites (24.0%, $N = 6$) ($\chi^2 = 5.61$, $df = 1$, $P = 0.018$). Raptors perching on riparian corridors were often flushed by the observer conducting the transect, due to the proximity of the walking transect to the riparian area. However, this occurred in both trail and control sites, and did not appear to change overall habitat use by raptors. Throughout the study period, there was no evidence for a temporal change in perching distances from riparian corridors in control ($F = 0.12$, $df = 1$, 27, $P = 0.74$) and trail sites ($F = 0.62$, $df = 1$, 24, $P = 0.44$).

Table 1. Habitat characteristics ($\bar{x} \pm SE$) for trail and control sites, Boulder County, CO, December 1995–March 1996. For riparian canopy composition, each species is reported as the percent occurrence sampled at control and trail sites ($N = 72$). Percent ground cover is the percent sampled within 1 m² radius points at control and trail sites ($N = 72$).

SITE CHARACTERISTICS	TRAIL	CONTROL
Riparian canopy:		
<i>Populus sargentii</i>	45.8 ± 9.6	37.5 ± 16.7
<i>Salix</i> spp.	26.4 ± 8.4	33.3 ± 7.2
<i>Elaeagnus angustifolia</i> ^a	6.3 ± 3.7	23.6 ± 12.1
Dbh (cm)	26.4 ± 4.3	25.5 ± 1.8
Grass cover (%)	81.4 ± 8.7	83.9 ± 0.7
Bare ground (%)	14.4 ± 7.4	15.7 ± 0.6
Shrub cover (%) ^a	4.2 ± 1.5	0.4 ± 0.2
Perches/ha	1.7 ± 0.3	2.7 ± 0.8

^a $P < 0.05$.

Habitat Sampling. Three species of trees, *Populus sargentii*, *Salix* spp., and *Elaeagnus angustifolia* comprised 84.4% ($N = 123$) of all trees sampled along riparian corridors at all sites (Table 1). *P. sargentii* did not differ in the percent sampled between control and trail sites ($\chi^2 = 0.60$, $df = 1$, $P = 0.438$), nor did the total number of *Salix* spp. ($\chi^2 = 0.86$, $df = 1$, $P = 0.354$). However, the percent sampled of *E. angustifolia* was greater in control sites, due to the riparian canopy of one site being predominately comprised of this species ($\chi^2 = 4.02$, $df = 1$, $P = 0.045$). The dbh of trees sampled along each riparian corridor did not differ between control and trail sites (ANOVA: $F = 0.08$, $df = 1$, $P = 0.777$).

The surrounding vegetation at five of the sites consisted primarily of grazed shortgrass prairie. One trail site consisted primarily of tallgrass prairie. The percent of ground cover sampled was predominately either grass, bare ground (no cover), or broad-leaf shrubs. Grass cover did not differ between control and trail sites (ANOVA: $F = 0.42$, $df = 1$, $P = 0.520$), nor did the percent of bare ground (ANOVA: $F = 0.13$, $df = 1$, $P = 0.723$). Shrub cover was greater at trail sites than at control sites (ANOVA: $F = 5.51$, $df = 1$, $P = 0.020$). However, shrub cover comprised <5% of all ground cover sampled (Table 1). The surrounding perch densities were similar between control and trail sites (ANOVA: $F = 1.59$, $df = 1$, $P = 0.276$).

DISCUSSION

Human activity associated with recreational trails in our study area may have affected wintering raptor populations, in terms of species richness, abundance and perch use. Species richness was consistently greater in control areas, with few raptors other than Red-tailed Hawks being observed at trail sites. The abundance of total raptors was more than three times greater in areas without trails, and those raptors observed in areas containing trails perched farther from riparian corridors. Habitat characteristics at trail and control sites were generally similar in both riparian canopy composition and dbh, and in the surrounding grassland habitat. Perch density was also similar in control and trail sites. A predominant difference in trail and control sites was the presence or absence of a recreational trail. Prior research has indicated that humans approaching on foot may affect raptors more than vehicle disturbance (Holmes et al. 1993), but no research to date has correlated the potential effects of recreational trails on raptor distribution and abundance.

The potential effects of recreational trails on raptors may be species-specific. Abundance of Bald Eagles was greater at control areas. Bald Eagles avoiding areas of human activity has been documented (Stalmaster and Newman 1978, Fraser et al. 1985), but we are unaware of any previous studies documenting recreational trail effects on Bald Eagles. Abundance of Red-tailed Hawks did not differ between control or trail sites. This was the only species of raptor commonly observed in trail areas. Red-tailed Hawks are generalist raptors, both in diet (Errington 1933, Hansen and Flake 1995) and in distribution (Brown and Amadon 1968). Knight and Kawashima (1993) observed Red-tailed Hawks exploiting power lines more often than expected, while Minor et al. (1993) found no significant differences in density and productivity of Red-tailed Hawks in urban and nonurban environments. In Boulder County, both wintering and breeding distributions of Red-tailed Hawks have not been sensitive to landscape urbanization (Berry et al. 1998). These studies suggest that Red-tailed Hawks have adapted to human development and associated activity. Our study suggests that Red-tailed Hawks tolerate human activity along recreational trails. Although our sample size was small for species of raptors other than Red-tailed Hawks and Bald Ea-

gles, overall these species were more abundant in areas with no recreational trails.

Perch use in control and trail sites varied greatly in our study, where the mean perch distance of raptors from riparian corridors was greater in trail sites. Although the overall density of perches outside of the riparian areas was similar between control and trail sites, we did not quantify raptor perching distance in relation to the distribution of potential perches from corridors. Nevertheless, raptors did use riparian corridors for perching more in control areas than in trail areas. Other research also indicates that riparian areas are used frequently by raptors, both for wintering habitat (Lingle 1989, Smallwood et al. 1996) and for nesting (Hansen and Flake 1995). Our study suggests both that riparian corridors are important areas for wintering raptors and that trails may displace raptor perch use away from riparian habitat.

One potential reason for differences in raptor abundance between trail and control sites could be from the increased shrub cover on trail sites. An increase in shrub cover could affect hunting strategies of raptors and could conceal prey, making prey less vulnerable (Craighead and Craighead 1956, Wakeley 1978). However, because shrub cover comprised <5% of all ground vegetation sampled, it is unlikely that this variable would control for the large differences of raptor abundance we observed.

The distribution of prey items may affect raptor distribution (Plumpton and Andersen 1998). We did not quantify prey availability at our sites. Prairie dog colonies, which are an important prey base for Bald Eagles, Red-tailed Hawks, and Ferruginous Hawks (Jones 1989), were not present at any of our sites. Distances to the closest prairie dog town were similar for both control and trail sites. Because distances were similar among sites, we believe that prey availability for these larger raptors did not confound our results. If these species were concentrating hunting efforts on prairie dogs, then foraging activities may have been infrequent in our sites. Smaller rodents, such as voles (e.g., *Microtus ochrogaster*), are important prey items for Rough-legged Hawks and Northern Harriers. Although vegetation was generally similar for control and trail sites, we cannot ascertain if vole populations were different among sites.

Because of large home ranges and movement ability of wintering raptors, effects of human activity and urbanization on wintering raptors should

be viewed with a landscape context (Berry et al. 1998). In areas of human activity, other factors affecting wintering raptors in the landscape could be mitigated, such as enhancing foraging opportunities (Preston and Beane 1996) or increasing perch availability (Widen 1994).

Buffer zones have been suggested as a means to reduce conflicts between human activities and raptor populations (Stalmaster and Newman 1979, Knight and Skagen 1988, Holmes et al. 1993). Although prior research has documented potential buffer zones for wintering raptors (Holmes et al. 1993), future research should focus on determining appropriate buffer zones from recreational trails and other specific types of human activity during the nonbreeding season. The type of activity should be considered because different effects could potentially occur from different types of activity (Preston and Beane 1996). By integrating perch availability (e.g., Marion and Ryder 1975), habitat type, prey abundance, and types of human activity, suitable indices for predicting optimal raptor environments and also appropriate buffer zones may be determined.

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SHORT COMMUNICATIONS

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NORTHERN GOSHAWKS NESTING ON A PRIVATE INDUSTRIAL FOREST IN WESTERN WASHINGTON

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KEY WORDS: *Northern Goshawk*; *Accipiter gentilis*; *nest*; *habitat*; *productivity*; *nesting density*; *forestry*; *Pacific Northwest*.

Very little is known about Northern Goshawk (*Accipiter gentilis*) nesting on private, intensively-managed timberlands in the Pacific Northwest. Previous information about goshawk nesting on the west side of the Cascades (Fleming 1987, U.S. Forest Service 1994) is known primarily from pristine National Parks and Wilderness Areas, as well as National Forest lands which have generally received light to moderate levels of timber harvesting since European settlement.

In 1995, the Murray Pacific Corporation implemented a multi-species Habitat Conservation Plan (HCP) which requires periodic monitoring of goshawk populations on their Mineral Tree Farm in Lewis County, Washington U.S.A. (Beak Consultants Incorporated 1995). To meet the requirements of the HCP, we designed and conducted a monitoring plan to determine the occupancy and breeding status of goshawks in all suitable and marginal nesting habitats on the tree farm. Additional information was obtained on goshawk breeding density, productivity, prey, nest sites, and habitat characteristics which are also presented.

STUDY AREA AND METHODS

The study area was the Mineral Tree Farm in Lewis County, WA, an industrial tree farm of about 21 600 ha in size which is owned and operated by the Murray Pacific Corporation. The tree farm is located along the western edge of the Southern Cascade Physiographic Province (Franklin and Dyrness 1984) and ranges in elevation from approximately 300–1640 m. Approximately 19 600 ha of the tree farm are capable of supporting forest, with the remaining area containing rocky ridgetops, alpine meadows, cliff/talus slopes, roads, brush, standing water and gravel pits. The study area falls within the Western Hemlock (*Tsuga heterophylla*) Forest Zone (Franklin and Dyrness 1984), which is dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock. Western red cedar (*Thuja plicata*) is locally abundant while Pacific sil-

ver fir (*Abies amabilis*) and noble fir (*A. procera*) are present at higher elevations. Commercial timber production is the dominant land use on the Mineral Tree Farm. In 1994, the landscape was covered by stands of various age classes including: recent clearcuts (0–5 yr old; 12%), saplings (6–26 yr old; 43%), pole forest (27–45 yr old; 28%) and commercially mature forest (>45 yr old; 15%). Scattered patches of remaining old-growth forest (250+ yr old) were lumped into the mature forest category because they were rare (<2%) and most (55%) had experienced partial (<50%) overstory removal within the past 80 yr. The area is characterized by a mild, wet maritime climate. Precipitation occurs mainly in winter and averages 1.8–3.6 m annually (Cummins et al. 1975).

Murray Pacific's Geographic Information System (GIS) timberlands database was queried to identify areas of potentially suitable goshawk nesting habitat on the Mineral Tree Farm. We divided habitat in two categories: (1) *suitable habitat* was considered any conifer-dominated stand ≥ 45 yr of age and (2) *marginal habitat* was considered any young coniferous stand 27–44 yr old or any stand of alder/hardwoods. Alder stands were dominated by red alder (*Alnus rubra*) and often contained a minor cohort of big-leaf maple (*Acer macrophyllum*) and black cottonwood (*Populus trichocarpa*), especially in riparian areas.

Surveys for nesting goshawks were conducted over the entire tree farm in 1995 and 1996 on all suitable and marginal habitat stands. In addition, we conducted a pilot survey for goshawks on the tree farm in 1994 (Bosakowski and Vaughn 1996) that was limited only to mature conifer habitat (28 cm dbh [diameter at breast height], 24 m height, 250–750 trees/ha, $\geq 70\%$ conifer composition). The protocol for surveys is described in Bosakowski and Vaughn (1996) and includes several modifications to the current U.S. Forest Service protocol for surveying goshawks in the Pacific Northwest (Appendix B in U.S. Forest Service 1994).

Nest site habitat attributes were measured from 15-m radius circular plots centered on nest trees. All trees and snags (dead trees) ≥ 10 cm in diameter within the plot were measured for dbh with a diameter tape and were identified to species. Heights of nests and nest trees were measured with a clinometer. Maximum slope through the nest site was measured with a clinometer and slope aspects were recorded. The presence or absence of canopy cover at 20 points was determined with an ocular sighting tube (James and Shugart 1970). The 20 points were systematically positioned with five points along each of the four cardinal directions at 10-m intervals. At each

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Table 1. Characteristics of nest trees and nest sites for three Northern Goshawk territories on the Mineral Tree Farm in the Western Washington Cascades.

PARAMETER	SNOW CREEK	EAST FORK TILTON	MINERAL CREEK	MEAN (SD)
NEST TREE				
Species	Douglas-fir	Western hemlock	pacific silver fir	
Nest height (m)	13.7	14.7	13.4	13.9 (0.68)
Nest tree height (m)	39.2	30.6	21.0	30.3 (9.10)
Nest tree dbh (cm)	53	73	41	55.7 (16.17)
NEST SITE ^a				
dbh (cm)	29	32	24	25.5 (2.94)
Canopy cover (%)	80	90	90	86.7 (5.77)
Shrub cover (%)	20	20	45	28.3 (14.43)
Live tree density (≥10 cm)(no./ha)	496	665	1132	764 (329.4)
Snag density (#/ha)	155	298	298	250 (82.56)
Sapling density (5–10 cm)(no./ha)	0	62	170	77.3 (86.0)
Pacific silver fir density (no./ha)	0	298	482	260 (243.2)
Red alder density (no./ha)	58	0	410	156 (221.9)
Western hemlock density (no./ha)	368	352	240	320 (69.74)
Douglas-fir density (no./ha)	70	15	0	28.3 (36.85)
Elevation (m)	600	745	975	773 (189.1)
Slope (%)	46	42	20	36 (14.0)
Slope aspect	N	N	NE	—
Stand age (yr)	40	54	43	45.7 (7.37)
qdbh (cm)	29	34	22	28.3 (4.04)
Patch size (ha) ^b	421	559	210	396.7 (175)

^a Measurements within a 15-m radius circle.
^b Nest stands were silvicultural units at least 33 ha as delineated from previous even-aged timber harvests, but all formed a contiguous forest patch mosaic with other closed-canopy stands of various ages ≥27 yr.

point, the presence or absence of shrub/sapling cover within arms' reach was also noted (Collins et al. 1982). Only woody stems ≥0.5 m in height and <10 cm dbh were considered shrub/sapling cover.

Stand-level data were obtained from recent stand inventory records for stand age and stand quadratic mean diameter at breast height (qdbh). Qdbh was calculated using all trees ≥10 cm dbh with the formula: qdbh = square root ((basal area/trees per ha)/0.005454).

A landscape-level spatial analysis with GIS was used to calculate the proportion of closed-canopy forest cover (≥27 yr) and mature forest cover (≥45 yr) within concentric circles at increasing distances (radii) from the nest. The range of distances tested was 0.2–3.2 km from the nests and was inclusive of the 2400-ha home range, 240-ha territory or postfledging family area (PFA) and 12-ha nest site as defined by Reynolds et al. (1992) for the Northern Goshawk in the southwestern U.S.

Prey remains were found under nests or at nearby prey-plucking posts. These were identified and enumerated using standard methods described by Reynolds and Meslow (1984).

RESULTS

During the 1994–96 study period, we found goshawks nesting in three different territories on the Mineral Tree Farm. Only one nest was occupied in 1995 (Mineral Creek), producing at least one fledgling. In 1996, three different occupied nests were monitored, each producing two fledglings for a productivity rate of 2.0 young fledged per nesting attempt. Overall, the nesting results translated into a nesting density ranging from 0.0046–0.0139 nests per 100 ha.

Nest stands were 40–54 yr old and were dominated by conifers (Table 1). Nest stands were densely stocked (496–1132 live trees/ha) on north-facing slopes with high canopy cover (80–90%), low to moderate shrub/sapling cover (20–45%) and high snag densities (155–298/ha). We attributed high snag densities to high suppression mortality, since all stands were still within the stem exclusion stage (Oliver and Larson 1990) for unmanaged (never thinned) second-growth stands in western Washington. At the densest nest site (Mineral Creek),

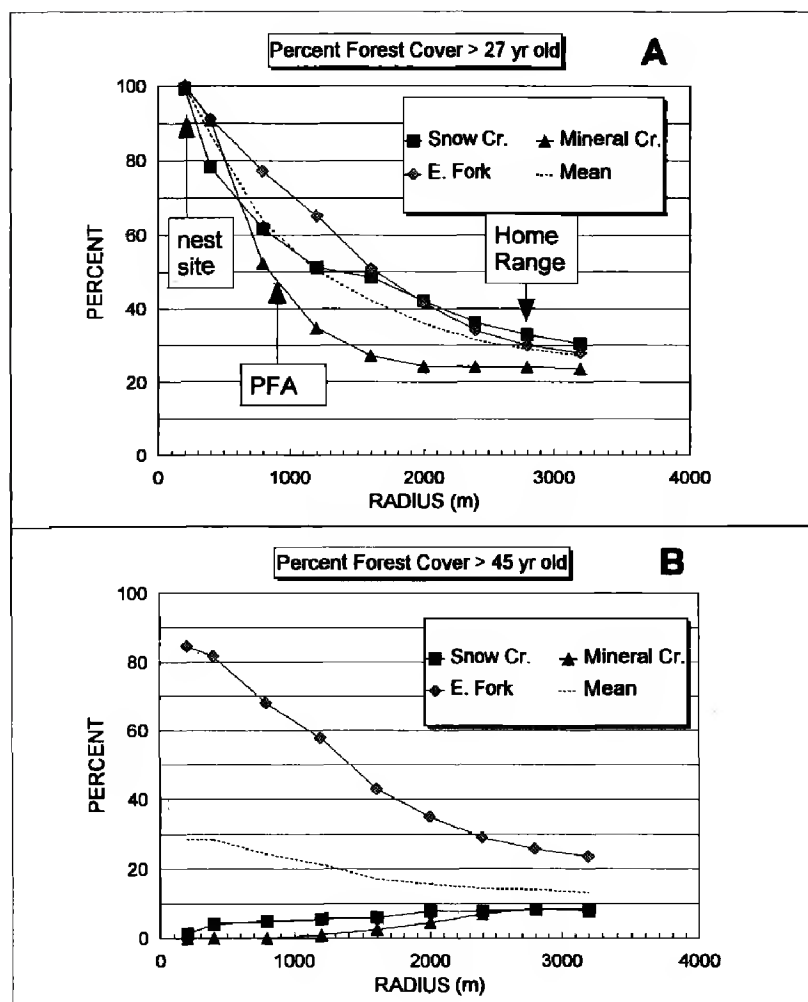


Figure 1. Percent forest cover at increasing distances (circle radii) from three Northern Goshawk nests on the Mineral Tree Farm in western Washington in 1996. Note that the data in Fig. 1a (top graph) is for all forest cover ≥ 27 yr and is inclusive of the data shown in Fig. 1b (bottom graph) for all forest cover ≥ 45 yr. The postfledging family area (PFA) is as described in Reynolds et al. (1992).

the nest tree was located on an old, overgrown logging road where the forest was more open and had a higher component of alder. In all cases, nests were built in dominant trees (mean dbh = 55.7 cm) of the stands which averaged only 28.3 cm in qdbh. Nest heights were consistently similar (range = 13.4–14.7 m), despite different nest tree heights and stand ages/types.

All nests were in large contiguous forest patches (range = 210–559 ha) comprised of a mosaic of closed-canopy forest (suitable and marginal habitat) of various ages and tree compositions. Landscape-level analyses of the three goshawk nests showed a similar trend for the amount of closed-canopy forest (Fig. 1a), with mean values of 100% forest cover within 196 m of the nest ("nest site"), 60% cover within 880 m ("PFA") and 30% cover within 2780 m ("home range"). However, the same trend was not apparent for older forest (Fig. 1b), where two of three territories had $< 10\%$ mature forest cover > 45 yr old. All nests were > 1.6 km from other landowners and within this distance, there was no old-growth forest at Mineral

and Snow Creek nests and only 45 ha at the East Fork nest.

A total of 37 prey items were recorded with grouse representing the most numerous prey item (56.7%). Although we did not differentiate between Blue Grouse (*Dendragapus obscurus*) and Ruffed Grouse (*Bonasa umbellus*) in most cases, Blue Grouse were detected at 25% of point counts whereas Ruffed Grouse were detected at only 5% of point counts on the tree farm (Bosakowski 1997). Steller's Jays (*Cyanocitta stelleri*) were the second most numerous prey items (16.2%), followed by snowshoe hare (*Lepus americanus*, 8.1%) and Northern Flicker (*Colaptes auratus*, 5.4%). Prey items found only once were Pileated Woodpecker (*Dryocopus pileatus*), Varied Thrush (*Ixoreus naevius*), Swainson's Thrush (*Catharus ustulatus*) and Gray Jay (*Perisoreus canadensis*).

DISCUSSION

We found goshawks nesting successfully in younger and denser stands than previously reported for northwestern goshawks (Reynolds 1983, Fleming 1987, Reynolds 1989, Marshall 1992). The spatial analysis revealed that closed-canopy conifer forest cover (≥ 27 yr old) was a consistent feature at the landscape level for all three nests, with 100% forest cover within the 12-ha nest site, about 60% cover within the 240-ha PFA, and about 30% cover within the 2400-ha home range. Plot samples showed that nest sites were composed of young (40–54 yr old) second-growth conifer-dominated forest with high tree and snag densities. None of these stands had received either commercial or pre-commercial thinning and average qdbh was low (28.3 cm) for goshawks even though saplings (trees < 10 cm dbh) were not included in the calculations. Previous measurements of goshawk nest sites in the western Washington Cascades have shown an average stand dbh of 48.3 cm and minimum of 34.5 cm (Fleming 1987).

Nesting stands in our study were at or younger than the usual harvest age (45–60 yr) for industrial forest land in western Washington. Growing conditions in the mesic Western Cascades fosters rapid tree growth, allowing suitable nesting habitat to develop in as little as 40 yr. This age is about half the minimum age (75 yr) needed for goshawk nesting habitat as predicted by a model developed in drier interior Douglas-fir forests of Idaho (Lilieholtm et al. 1993). Even though the nesting stands in this study were relatively young, it is noteworthy that all three of the nest trees were dominants or remnants (East Fork Tilton nest), having the largest (or second largest) diameter in the sample plot. Similarly, Fleming (1987) also noted that in younger second-growth stands, goshawks usually selected the largest trees to provide suitable support for the large, heavy nest since larger trees are more likely to have thicker, stronger support branches. These studies indicate the value of remnant trees (residuals) for goshawks and confirm a definite benefit to

maintaining green leave-tree clumps and individual trees after timber harvesting.

We noted that grouse were more prevalent in the diet on the tree farm in comparison to Northwest National Forests, where goshawks relied primarily on forest-interior species (Reynolds and Meslow 1984, Bull and Hohmann 1994). Since one of the principal foods of the Blue Grouse is Douglas-fir needles (Martin et al. 1951), we speculate that replanting clearcut areas with (primarily) Douglas-fir may have helped support successful goshawk nesting under less than optimal habitat conditions.

Our finding of three occupied nests in 1996 on the Mineral Tree Farm represents a nesting density of about one-half to one-fourth of the nesting density that we calculated for three to seven occupied nests located by DeStefano et al. (1994) on the Wallowa-Whitman National Forest in the Oregon Cascades. At least in one year, goshawk reproduction on the Mineral Tree Farm was similar or higher than reproduction occurring in more pristine National Forests of Oregon (DeStefano et al. 1994, Bull and Hohmann 1994). Overall, this study suggests that goshawks may be breeding more commonly on private industrial forests than previously predicted, which might be contributing substantially to the regional population of goshawks. In the Cascades of Washington and Oregon, the frequent intermingling of National Forest land and private industrial timberland further underscores the importance of managing for goshawks under both types of ownerships.

RESUMEN.—Esta investigación reveló que *Accipiter gentilis* anidó en un bosque comercial privado (21 600 ha) en el Condado de Lewis, Washington, Estados Unidos. El número máximo de nidos activos fue de 1–3 lo que se traduce a una densidad de 0.0046–0.0139 nidos por 100 ha. Cada uno de estos tres nidos produjo dos juveniles en 1996, para una productividad de 2.0 juveniles por intento de anidación. Los árboles del nido eran coníferas de 40–54 años. Todos los nidos estaban ubicados en parches continuos de bosque (entre 210–559 ha) que incluían un mosaico de dosel cerrado (>27 años) de distintas edades y composiciones. Los niveles de análisis de paisaje de los tres nidos revelaron una tendencia similar en relación a la cantidad de bosque de dosel cerrado (>27 años), con valores medios del 100% de cobertura boscosa dentro de 196 mts del nido (sitio del nido), 60% de cobertura dentro de 880 mts (área de la familia posterior a la eclosión) y 30% de cobertura dentro de los 2.780 mts (rango de hogar). Sin embargo, este mismo patrón no es aparente en bosques mas antiguos donde dos de los tres territorios tenían <10% de cobertura madura (>45 años) dentro de su rango de hogar.

[Traducción de César Márquez]

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NOTES ON EGGS OF THE BICOLORED HAWK *ACCIPITER BICOLOR*

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KEY WORDS: *Bicolored Hawk*; *Accipiter bicolor*; eggs; nest; Neotropical raptor.

Little is known of the breeding habits of Neotropical accipiters, including the widely distributed, but inconspicuous, Bicolored Hawk (*Accipiter bicolor*). From 1991–94, we conducted a study of the breeding biology of this species in Tikal National Park in NE Guatemala. Here, we provide details on Bicolored Hawk eggs found at Tikal and compare them to earlier published descriptions, including some that were probably misidentified.

Fourteen Bicolored Hawk eggs from six nests at Tikal were dull white, unspotted, nonglossy and subelliptical in shape (Preston in Palmer 1962). The inner surface of the shells had a light bluish or greenish tinge, as is typical of many *Accipiter* species (Bent 1937, Schönwetter 1961). As measured in the field with Vernier calipers, they averaged 47.1 ± 1.1 mm (\pm SD, range = 44.9–49.0) \times 36.5 ± 1.1 mm (range = 35.0–38.6), and the average mass of eggs at various stages of incubation was 33.5 ± 3.5 g (range = 28.0–38.0), as taken with a 100 g Pesola spring scale. Overall, the eggs closely resembled those of the related Cooper's Hawk (*Accipiter cooperii*), aside from their slightly greater "elongation" (length/breadth ratio) (i.e., 1.29 [this sample] vs. 1.26 [$N = 172$ for the Cooper's Hawk, Kiff unpubl. data]). Only clutches of 1–3 eggs were observed at Tikal with an average clutch size of 2.4 eggs.

These details differ from some published descriptions of Bicolored Hawk eggs and museum specimens attri-

buted to this species, but they agree with others (Table 1). In order of their collecting year, other purported eggs of this species include the following: Chubb (1910) reported that three eggs, probably representing a single clutch, of the race *A. bicolor pileatus*, taken in Paraguay (locality unknown) on 19 October 1902 were "dull white without any markings beyond a few underlying cloudings of a somewhat darker tint." They measured 1.8–1.9 in (46–48 mm) \times 1.4–1.5 in (36–38 mm), thus agreeing closely with the Bicolored Hawk eggs from Tikal. Based on these sparse details, there is no reason to doubt the authenticity of these eggs.

A set of two purported Bicolored Hawk (*Accipiter b. bicolor*) eggs taken near Bartica, British Guiana on 13 April 1927 for the British collector G.D. Smooker is in the Western Foundation of Vertebrate Zoology collection (WFVZ 16 695). According to the accompanying data, the species identity was based on a description of the birds. The eggs were in an advanced stage of incubation, and the nest was said to be "composed of sticks and placed high up in a tree—no further particulars given." The egg measurements were noted on the data card as 42.0×32.8 and 42.6×33.1 mm. The collector of the set was noted as "a native," probably indicating that Smooker did not visit the nest himself. Other misidentified raptor eggs have been reported from the Belcher-Smooker Trinidad collection (e.g., Boyce and Kiff 1981, French 1973, Kiff 1981); thus, all records from Smooker, who evidently relied heavily on native collectors, should be viewed with caution.

Table 1. Comparison of Bicolored Hawk (*Accipiter bicolor*) eggs from Guatemala with earlier published accounts and unreported museum specimens. See text for additional details on egg appearance and nests.

AUTHORITY (YEAR) (N)	LENGTH (mm)	BREADTH (mm)	COUNTRY (YEAR COLLECTED)	PROBABLE AUTHENTICITY
This study (N = 14)	47.1 (44.9–49.0)	36.5 (35.0–38.6)	Guatemala (1991–93)	Authentic
Chubb (1910) (N = 3)	46–48	36–38	Paraguay (1902)	Authentic
G.D. Smooker (WFBZ 16 695)	42.02, 42.75	33.06, 33.31	Brit. Guiana (1927)	Misidentified
Hewitt (1937)	38	32.75	Venezuela (1936)	Misidentified
Housse (1945)	44	34	Chile (year?)	Indeterminate
Schönwetter (1961)	37.0, 41.3	31.0, 32.6	Not given	Misidentified
Schönwetter (1961)	46.5	35.2	Ecuador (1961)	Authentic?
Wolfe (1964) (WFBZ 16 694)	46.27	36.15	Mexico (1961)	Authentic
F.F. Nyc, Jr. (WFBZ 145 391)	46.9, 48.4	36.4, 36.1	Mexico (1970)	Authentic

This set was mentioned by Wolfe (1964), who described their appearance as a “grayish white ground color and both are sparingly flaked with light yellowish brown.” He gave the measurements as 42.0×32.8 and 42.6×33.1 mm. This set was reexamined in October 1998, and similar measurements (41.02×33.06 and 42.75×33.31 mm) were obtained. Both eggs are short subelliptical in shape (Preston *in* Palmer 1962), and they are dull white with faint light brown splotches and darker brown markings that may be nest stains. Since they differ so conspicuously in both color and size from the Tikal eggs, they were almost certainly misidentified.

Hewitt (1937) attributed a single egg taken on 28 April 1936 in the Rio Orinoco District, Venezuela to the Bicolored Hawk. The egg was white with faint nest stains and was marked with thin, rust-colored streaks (interpreted as pigmentation, although they were probably blood stains). It was said to exhibit a greenish tinge when held before a strong light. It measured only 38×32.75 mm, thus being about one-third smaller in volume and much more spherical (elongation = 1.16) than the Tikal eggs of this species. The nest was described as a small cup composed of dry sticks and lined with a few leaves and situated at the end of a branch 50 ft above the ground. The bird was said to have been identified on the nest. Seventeen Bicolored Hawk nests at Tikal were located in forks in main tree trunks, where they were supported by large branches or vines, or near the tops of trees supported by several strong branches. None were found at the end of branches, a nesting situation more typical of several Neotropical kite species, and all were well-concealed from below. As Hewitt was not known to have personally collected eggs in South America, he presumably obtained the specimen from some other collector or

(more likely) from a commercial dealer. Given these discrepancies, we conclude that this specimen was misidentified.

Housse (1937) provided various unconvincing details on nests and eggs purportedly of the Chilean race, *Accipiter bicolor chilensis* (often regarded as a separate species, e.g., Johnson 1965, del Hoyo et al. 1994). Nests of the species were said to usually be in the forks of tall trees inside the forest, but close to a clearing or open country, and made of dry or green twigs, closely interlaced and lined with dry grass so as to provide a smooth and rounded finish to the inner cup. Housse claimed that four eggs was the usual clutch, but that there were sometimes even five or six eggs in a nest. The eggs were described as nearly elliptical, smooth but somewhat thick-shelled, white with large yellowish or greenish blotches concentrated around the larger pole and with numerous small yellow and gray spots elsewhere. Measurements were given as 44×30 mm in the earlier reference (Housse 1937), but as 44×34 in Housse (1945). The clutch size, egg measurements, color of egg markings and the nest description is more suggestive of some other species, perhaps the Chimango Caracara (*Milvago chimango*); at least they do not agree in these details with known authentic Bicolored Hawk eggs and nests. It is worth mention that the egg size and color description given in the Bicolored Hawk species account in Brown and Amadon (1968), which seem to be for *A. bicolor chilensis*, were actually those from Wolfe’s (1964) description of Mexican eggs.

Schönwetter (1961) gave the measurements of two purported eggs of the race *A. bicolor pileatus* as 37.0×32.6 and 41.3×32.6 mm, far below the likely range of measurements for eggs of the Bicolored Hawk. No details on locality or collector were provided. Another egg listed

by Schönwetter, apparently from western Ecuador and said to be from the Pässler collection, has more credible measurements of 46.5×35.2 mm, and based solely on these data, it may be authentic. Because the size of this specimen differed from the one reported by Hewitt (1937), Wetmore (1965) regarded (wrongly, we think) the former specimen as genuine and this one as misidentified. This egg would be from the nominate race *bicolor*, although birds from western Ecuador have sometimes been regarded as a separate race, *A. b. schistochlamys* (cf. Hellmayr 1949).

Wolfe (1964) described an egg of the race *Accipiter bicolor fidens* he collected in northern Veracruz, Mexico on 6 May 1961, with the assistance of R. Reyes, as "very light bluish gray without markings." He gave the measurements as 46.2×36.1 mm. This specimen is in the Western Foundation of Vertebrate Zoology collection (WVZ 16 684), where it now appears as dull white, lacking pigment, but with some faint nest stains. It is subelliptical in shape. The nest was placed about 80 ft (24.4 m) from the ground in an old nest of the Common Black-hawk (*Buteogallus anthracinus*) in thick woods along a stream. The old nest had been lined with a few small twigs and some green leaves. Wolfe was a well-respected authority on raptors and their eggs, and there is no question that this egg is authentic. The original color of the egg, i.e., "light bluish gray," is typical of many fresh-laid Cooper's Hawk eggs (Bent 1937), but the bluish color fades during incubation. Wolfe's specimen was "fresh" when it was collected.

The Western Foundation collection contains another set (WVZ 145 391) taken by the late Fred F. Nyc, a Texan oologist who made frequent collecting forays into Mexico from the 1940s to the early 1970s, often in the company of fellow oologists Col. Wolfe and Dr. Travis Meitzen. We knew Nyc well and judged him to be a reliable, knowledgeable collector. According to the accompanying data card, Nyc collected the set about 12 mi (19.3 km) southwest of Tampico, Tamaulipas, Mexico "in the oil fields" on 20 March 1970. The eggs were fresh, and the collector suspected that the set was incomplete. Identification of one (or both?) of the birds was based on a half hour of observations with binoculars from a distance of 50 ft. The nest was described as about 10 ft (3.1 m) high in a "straggly" mesquite tree in open country, and it was lined with grass and a few green leaves.

We examined and measured the Nyc eggs on 18 October 1998. Their shape is subelliptical, and they measure 46.85×36.32 and 48.36×36.02 mm. Both are dull white with a sprinkling of fine brown spots on the large end; one of the eggs is more heavily marked than the other. In all details other than the markings, the egg is virtually identical to one (WVZ uncat.) we collected at Tikal, although it also bears dark nest stains which might be interpreted as pigmented markings. Faint brown spots and splotches, many below the outer cuticle and often heavier at the larger end, are typical of Cooper's Hawk eggs

(Bent 1937, Palmer 1962), so it is not unlikely that some Bicolored Hawk eggs also bear such markings.

The coastal locality and the open habitat, unlikely for this deep forest species (Howell and Webb 1995), might cast doubt on the authenticity of this set, or at least on the associated data. However, Nyc noted on the data card that he had found a nest of this species containing a clutch of five eggs in the same area on 20 May 1952. On this date, one of the eggs in this clutch had just hatched, two had pipped and the other two were addled. All were so badly oil-stained that Nyc expressed surprise that they could have remained viable. His field notes indicate that a bird was shot at the nest, presumably to identify it. A clutch size this large would be unexpected for a tropical accipitrid, but perhaps it is typical at the relatively high latitude of southern Tamaulipas.

In summary, we regard the specimens of Chubb (Paraguay), Nyc (Mexico) and Wolfe (Mexico) to be authentic, and the eggs reported by Schönwetter from Ecuador were probably authentic. Based on a comparison with the Tikal sample and other details, the eggs reported by Hewitt (Venezuela), Schönwetter (*A. b. pileatus*) and Smooker (British Guiana) were probably misidentified. The ambiguous details provided by Housse on eggs from Chile do not permit any conclusion to be drawn about their authenticity.

These examples illustrate both the strengths and weaknesses of museum collections. Younger researchers, who may not have grown up in a collecting tradition, should regard museum specimens as an essential resource, but they should view specimen data (especially for egg sets) with the same critical eye they would apply to any other data set. Ideally, all trained field workers in poorly studied regions should be encouraged to add material to museum collections as possible, even if only opportunistically from salvaged material, since even for such a widespread species as the Bicolored Hawk, which occurs from NW Mexico south to Tierra del Fuego, there is a dearth of usable oological specimens with reliable modern data.

RESUMEN.—Una comparación de las descripciones publicadas de huevos de *Accipiter bicolor* con las características 14 huevos conocidos en seis nidos guatemaltecos estudiados entre 1991–94, indica que muchos de los reportes anteriores fueron probablemente basados en la identificación equivocada de especímenes. Los huevos de *Accipiter bicolor* reportados en Paraguay (Chubb), México (Nyc, Wolfe) y Ecuador (Schönwetter) parecen auténticos, pero los especímenes de Venezuela (Hewitt) y Guyana (Smooker) están erróneamente clasificados. La identificación actual de huevos de Chile (Housse) es errada.
[Traducción de César Márquez]

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NESTING ECOLOGY OF RED-SHOULDERED AND RED-TAILED HAWKS IN GEORGIA

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KEY WORDS: *Red-shouldered Hawk; Red-tailed Hawk; Buteo lineatus; Buteo jamaicensis; reproductive success; nest-site reoccupancy; nesting chronology.*

Because forest raptors occupy the top of many food chains, have relatively large home ranges and have a history of human persecution, they generally are among the first groups of vertebrates to respond to alterations of habitat (Fuller 1996, Niemi and Hanowski 1997). Therefore, information on the biology and nesting ecology of forest raptors is needed to predict or mitigate possible impacts of habitat alterations associated with forest management practices. This is especially true in the southeastern U.S., where large areas are under intensive timber management and little is known about the regional biology of resident raptor species.

Although Breeding Bird Surveys indicate that resident populations of Red-shouldered (*Buteo lineatus*) and Red-tailed (*B. jamaicensis*) Hawks are stable or increasing in Georgia (Preston and Beane 1993, Crocoll 1994), little has been published concerning their nesting ecology in the southeastern U.S. Moorman and Chapman (1996) compared the macro- and micro-habitat factors that influence nest-site selection of the two species, and Howell and Chapman (1997) described the home range and habitat use of nesting Red-shouldered Hawks in central Georgia. Here, we present data on the nesting chronology, nesting success and nest reoccupancy rates for both species in Georgia.

STUDY AREA AND METHODS

Our study was conducted in 1994 and 1995 at the Bishop F. Grant Memorial Forest (BGMF), a 5718-ha state wildlife management area located in Putnam County, Georgia. The BGMF contains a diversity of habitat types including bottomland and upland hardwoods, various-aged pine stands and pastures (Moorman and Chapman 1996, Howell and Chapman 1997).

We searched for old hawk nests between January and

early March 1994, and returned beginning in mid-March to check for signs of nesting activity. We continued to search for occupied nests through mid-June 1994. We located hawk nests by searching areas where they were seen perching or soaring. To prevent bias, nest searches also were conducted in all forested stands with trees >20 yr old where birds were not seen or heard. Nests were considered occupied if incubating females down or young were observed in nests. Young could not be documented during ground visits until they were approximately 1 wk old. We monitored occupied nests of both species every 7–10 d and recorded the status (e.g., incubating, small young, large young). A nest was considered successful if it fledged at least one young. Actual fledging dates were calculated as the median day between the last visit when young were present in nests and the visit when nests were vacant. Because nests were found throughout the breeding season, data from the early portion of the nesting season was lacking for some pairs. Return visits were made during 1995 to check activity of 1994 nests and to make observations on hawk nesting ecology. Nest revisits began on 31 March 1995 and were continued every 10 d until the end of June.

RESULTS

Red-shouldered Hawk Nesting Ecology. Twelve Red-shouldered Hawk nests were found in 1994. Incubation was first observed on 24 March and it continued through 18 May at one nest. Nestlings were first observed on 25 April and most nests contained young by 7 May. Fledgling hawks were first observed on 5 June and all successful nests had fledged young by 25 June. Four nests failed to fledge young, two nests fledged one young and six nests fledged two young.

In 1995, we revisited 10 Red-shouldered Hawk nests used in 1994. The two other nests from 1994 either had been damaged or had fallen from trees at the end of the 1994 breeding season so they were not revisited in 1995. We located occupied nests in six of the 10 nesting territories used the previous year. Two pairs repaired and used alternate nests within the same breeding territory occupied in 1994, and four others reused 1994 nests. Three female hawks were banded and radio-collared in 1994 (Howell and Chapman 1997). In 1995, banded birds were seen entering or leaving nests in all three ter-

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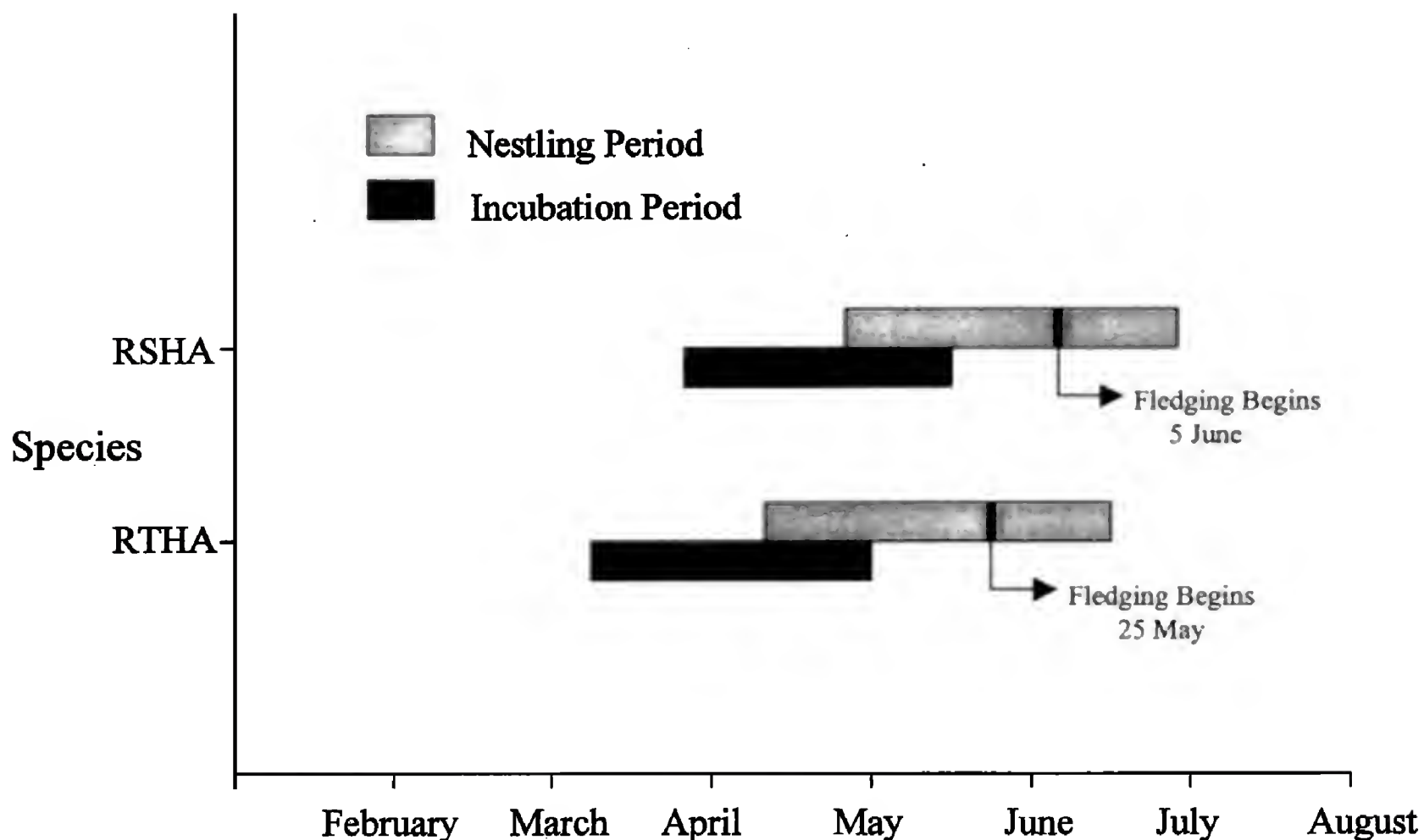


Figure 1. Nesting chronology of Red-shouldered (RSHA) and Red-tailed Hawks (RTHA) in Georgia.

ritories in which females were marked during the previous season, indicating that the same females reoccupied nests used in 1994. Nesting activity in 1995 was first observed on 6 April. Red-shouldered Hawk young were first observed on 18 April and all nests contained nestlings by 12 May. All Red-shouldered Hawk young fledged by 25 June. One nest failed, four nests fledged two young and one fledged three young.

Red-tailed Hawk Nesting Ecology. Ten Red-tailed Hawk nests were located during the 1994 breeding season. Signs of incubation were first observed on 7 April but, because we failed to locate most Red-tailed Hawk nests early in the nesting season, incubation probably started earlier. Nestlings were first observed on 15 May and an unfledged nestling was last observed in a nest on 15 June. Fledglings were first observed on 14 June and most remained near the nest for several more weeks. Five of 10 Red-tailed Hawk nests fledged one young. Remains of dead nestlings were found under two of the nests that fledged young.

Eight Red-tailed Hawk nests used in 1994 were revisited in 1995. The two other nests from 1994 were not revisited for logistical reasons. Six of eight 1994 Red-tailed Hawk nests were reoccupied. One nest occupied by Great Horned Owls (*Bubo virginianus*) in March 1995 was not used, although a pair of Red-tailed Hawks was observed repeatedly in the area during later visits that year. During

our initial visit on 31 March 1995, signs of incubation were observed at four of the nests used in 1994. Red-tailed Hawk nestlings were first observed on 12 May. Several of these nestlings were well developed and appeared to be approximately 2 weeks old. Fledgling Red-tailed Hawks were first observed on 6 June. Three of six nests fledged one young, two fledged two young and one nest failed.

DISCUSSION

Nesting chronology for both hawk species in Georgia likely varies by individual pair and year. However, on average, Red-shouldered Hawks begin incubation in late March, eggs hatch in late April to early May, and young fledge in early to mid-June (Fig. 1). Red-tailed Hawk nesting generally begins 2 wk earlier (Fig. 1). Burleigh (1958) reported incubation by a Red-shouldered Hawk as early as 22 March and as late as 1 May, and incubation by a Red-tailed Hawk as early as 15 February and as late as 10 April in Georgia. We documented later incubation dates for both species, although the birds observed incubating in our study might have been brooding small nestlings.

Red-shouldered Hawks often fledge up to four young, but the average number/breeding pair usually ranges from 1.1–1.8 (Crocoll 1994). Red-tailed Hawk nest success ranges from 58–93%, but the number of young fledged/breeding pair is usually between 1.0–1.5 (Pres-

ton and Beane 1993). During the 1994 breeding season, Red-shouldered Hawk nesting success (66%) and number of fledglings/breeding pair (1.17) were similar to that of previous studies, but Red-tailed Hawk nest success (50%) and number of fledglings/breeding pair (0.5) were lower than reports from other parts of North America. Red-tailed Hawk clutch sizes generally increase from south to north and from east to west (Henny and Wight 1972, Preston and Beane 1993), so the low productivity may not be unusual for the southeastern U.S. These low numbers also may suggest that prey abundance was low during the first year of our study (Preston and Beane 1993), but data on prey abundance were unavailable. Two dead young were found below Red-tailed Hawk nests in 1994, which may indicate nestling starvation or sibling aggression (Stinson 1980). Records from our return visits in 1995 indicated that nest success (83% and 83%) and number of fledglings/breeding pair (1.83 and 1.17) increased for both Red-shouldered and Red-tailed Hawks, respectively. However, our 1995 results could be biased because early nest failures or pairs in new territories were not monitored.

Breeding-site fidelity is common in both species (Bent 1937, Preston and Beane 1993, Crocoll 1994). In Wisconsin, Jacobs and Jacobs (1993) documented 50% nest reoccupancy and 83% territory reoccupancy by Red-shouldered Hawks. Burleigh (1958) reported one incident of traditional nest-site use by Red-shouldered Hawks and one account of nest-site reoccupancy by the Red-tailed Hawk in Georgia. However, nest-site reoccupancy rates have not been reported for the two hawk species in the southeastern U.S. Forty percent of the Red-shouldered Hawk nests used in 1994 were reoccupied in 1995, and Red-shouldered Hawks occupied alternate nests in at least two more of the 10 territories used in 1994 ($\geq 60\%$ territory reoccupancy). Seventy-five percent of the nests used in 1994 by Red-tailed Hawk pairs were reoccupied in 1995. We could not measure fidelity because hawks were not uniquely marked, but the presence of banded female Red-shouldered Hawks indicated that the same females returned to the nesting territories occupied the previous year.

Red-tailed Hawk breeding territories associated with ephemeral, early-successional habitats such as clearcuts may shift with changes in the vegetative structure of these stands. However, nests located near permanent openings such as pastures may be reoccupied for many consecutive years. Red-shouldered Hawks, which nest in mature, more permanent bottomland forests (Bednarz and Dinsmore 1981, Moorman and Chapman 1996), likely also maintain traditional territory boundaries for long periods. Conservation of areas containing traditional Red-shouldered Hawk breeding territories may help prevent replacement by Red-tailed Hawks (Bednarz and Dinsmore 1982).

RESUMEN.—La ecología de anidación de *Buteo lineatus* y *Buteo jamaicensis* ha sido poco conocida en el sureste de

los Estados Unidos. Documentamos la cronología de anidación, éxito de anidación y reocupación de nidos para ambas especies entre 1994–95. Durante la época reproductiva de 1994, el éxito de anidación (66%) de *Buteo lineatus* y de productividad (1.17 pichones/pareja reproductiva) fué muy inferior a los valores reportados anteriormente. Las nuevas visitas a los nidos y las observaciones adicionales en 1995, indicaron que el éxito reproductivo incrementó para las dos especies. Los cambios en el éxito reproductivo de las dos especies pudo haber sido causado por fluctuaciones en las poblaciones de presas. Las tasas de re-ocupación de nidos fueron del 75% y 40% para *Buteo jamaicensis* y *Buteo lineatus* respectivamente. La conservación de las áreas tradicionales de anidación puede ser requerida para mantener las poblaciones locales de gavilanes en reproducción.

[Traducción de César Márquez]

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THE RED KITE (*MILVUS MILVUS*) REINTRODUCTION PROJECT: MODELING THE IMPACT OF TRANSLOCATING KITE YOUNG WITHIN ENGLAND

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KEY WORDS: *Red Kite*, *Milvus milvus*; *reintroduction*; *translocations*; *England*.

The Red Kite (*Milvus milvus*) reintroduction project started in 1989 with the release of six Swedish kites at a site in northern Scotland and four Swedish and one Welsh kite at a site in southern England (Evans et al. 1991). From 1989–94, a total of 93 birds were released at each site with southern England birds coming mainly from Spain and northern Scotland birds from Sweden (Evans et al. 1997). As a result of these releases, small populations have been successfully established in both release areas. In 1997, the southern England breeding population reached about 55 pairs and is now considered to be self-sustaining.

In order to improve the status of Red Kites in Britain and to increase their spread to other suitable areas, releases have started at two new sites in central Scotland and the English midlands (Carter 1995). At the latter site, a total of 29 birds, mainly from Spain, were released in 1995 and 1996. In 1997, another 10 kites from Spain were released but, due to concerns about declines in the Red Kite population in parts of Spain, Spanish authorities decided that it would be difficult for them to supply kites for the project in future years. Discussions with the recently formed Welsh Kite Trust led to an agreement that young rescued from vulnerable nests and for which suitable foster nests could not be found within Wales would be made available for translocation to the English midlands release site. However, this would involve only a few birds and, in some years, no young would be available for the reintroduction project.

In order to make up this short-fall of birds for release, the translocation of young kites from the expanding southern England population was considered. To help assess the impact of any such translocations, we devised a simple model to show the likely effects on the southern England and midlands populations. Various scenarios were modeled, reflecting the range of options available.

METHODS

The model used the following data and assumptions based mainly on monitoring work on the expanding southern England kite population up to 1996 (Evans et al. 1997, N. Snell, M. McQuaid and P. Stevens unpubl. data): (1) 76% survival in the first year based on sightings of individually-identifiable, wing-tagged kites, released between 1989–94 ($N = 93$); (2) 93.5% adult survival based on sightings of individually-identifiable, wing-tagged kites in their second and subsequent years ($N = 136$); (3) breeding productivity of 2.1 young per breeding attempt between 1991–96 ($N = 94$); (4) balanced immigration and emigration (this seemed reasonable because Red Kites are known to have a very high level of natal philopatry [Newton et al. 1994]. No wing-tagged kites released or fledged in southern England have yet been found breeding elsewhere, although because some released birds have now lost their tags and not all young are fitted with tags each year, it is possible that a small number of cases have gone undetected; at least one continental immigrant is known to have been recruited into the southern England breeding population [I. Evans pers comm.]); (5) age of first breeding at two years (in the southern England population, kites have occasionally bred in their first year but normally attempt to breed for the first time in their second year; in Wales where the habitat is less suitable, kites have been recorded breeding

Table 1. Estimated number of breeding pairs of Red Kites in the southern England and the English midlands using the model assuming that 20 young kites are translocated from the southern England population.

YEAR	S. ENG.— DO NOTHING	S. ENG.—REMOVE 20 CHICKS IN 1997	MIDLANDS—RELEASE NO BIRDS IN 1997; 20 IN 1998 AND 1999	MIDLANDS—RELEASE 20 BIRDS EACH YEAR 1997 TO 2000
1997	50	50	3	3
1998	75	75	9	9
1999	108	100	11	18
2000	157	150	24	30
2001	227	215	37	48
2002	329	313	52	68

for the first time at up to seven years of age [Newton et al 1987]); (6) equal sex ratio (a population of 40 birds, two years or older was assumed to have 20 breeding pairs).

Since it was a simple, deterministic model, density-dependent effects and stochastic events were not taken into account, although their implications were considered.

The starting point for each scenario was the estimated kite population in southern England and the midlands in 1997, including the number of breeding pairs and the number of surviving young fledged from nests in 1996. For each year (x), the population in the following year ($x + 1$) was calculated by summing the following values derived from the data and assumptions: (1) number of breeding adults surviving from year x to year $x + 1$; (2) number of young fledged in year $x - 1$ surviving to breed for the first time in year $x + 1$; (3) number of young fledged in year x surviving to year $x + 1$. In each case, the number of young removed or added to the population under a given scenario was taken into account in (2) and (3).

RESULTS

Scenario 1. Remove 20 young from the southern England population in 1997 and release them in the midlands. We assumed that no further birds were translocated from southern England in subsequent years but 20 birds from an alternative donor population were released in the midlands in 1998 and 1999. By the year 2002, this

translocation resulted in an increase of 31% in the number of pairs in the midlands compared to the release of no birds in 1997 (Table 1). The removal of the 20 birds from southern England resulted in a 4.9% decrease in that population. The effect of releasing the extra birds in the midlands was most noticeable in the years 1998 to 1999 when the population increased from nine to 18 pairs as opposed to an increase from nine to only 11 pairs if no birds were released.

Scenario 2. In this scenario, no further birds were available for release in the midlands from sources outside southern England. Fifteen birds were taken from southern England and released in the midlands in each year between 1997–99. In this example, the release of 15 birds in the midlands each year between 1997–99 resulted in a 74% increase in the midlands population by 2002 compared to doing nothing (Table 2). The loss of the 15 birds in each of three years from southern England resulted in a population reduction from 328 pairs to 303 pairs in 2002, a difference of 8%.

In both the above scenarios, because the model does not take into account any density-dependent effects, the number of kites gained by the midlands population exactly matches the number lost to the southern England population. The percentage difference was, however, much greater for the midlands population than the well-established southern England population.

Table 2. Estimated number of breeding pairs of Red Kites in southern England and the English midlands assuming that 15 birds are taken from southern England and released each year from 1997–99.

YEAR	S. ENG.— DO NOTHING	S. ENG.—REMOVE 15 CHICKS IN 1997, 1998 AND 1999	MIDLANDS— DO NOTHING	MIDLANDS—RELEASE 15 BIRDS IN 1997, 1998 AND 1999
1997	50	50	3	3
1998	75	75	9	9
1999	108	102	11	16
2000	157	146	17	27
2001	227	207	23	42
2002	329	303	34	59

DISCUSSION

One of the requirements of any well-planned reintroduction project is that it should be adequately monitored (IUCN 1987). This not only ensures that any problems will be identified and resolved at an early stage but also facilitates decisions about the future of the project. Use of this simple model was only possible because the basic population and survival data were available from monitoring work on the southern England Red Kite population.

The model proved to be a valuable aid to decision making when considering the various options for translocating Red Kites for release in the midlands and, in particular, the option of taking birds from southern England in 1997. Having used the model to help consider the potential impact of translocating 10 birds in 1997, kite workers involved with the project agreed that the translocation should go ahead. It was accepted that the translocated birds would significantly improve the status of the small, vulnerable midlands population without having a significant impact on the larger donor population. In effect, the birds were thought to be more valuable in helping to meet the project's overall aim of restoring kites to all suitable habitats in Britain if they were translocated and released in the midlands. Ten young were taken under licence from nests in June 1997 and have been released into the midlands along with the 10 birds imported from Spain.

In order to minimize any impact on the southern England population, only the smallest young were taken from broods of two or three (broods of four occur only very occasionally). In one case, the two smallest young were taken from a brood of three. With many species of birds of prey and owls, the smallest young are vulnerable to being eaten by their siblings if there is a shortage of food (Newton 1979, Cramp and Simmons 1980, Cramp 1985, Watson 1997), and this has been recorded in the Welsh kite population (Lovegrove et al. 1990). Most deaths due to aggression from siblings would be expected when young are still small, and deaths are much less likely when the chicks are four wk or older, the age at which the kites were collected from nests. Nevertheless, it is still possible that some young taken from southern England would not have fledged successfully if left in nests. In captivity, it was possible to provide the young with a surplus of food and prevent any problems due to food shortage.

Because our model is purely deterministic, the year to year population changes were solely dependent on the set of population parameters derived from monitoring the southern England population. No possible effects of chance, stochastic, events acting on the population were considered. While chance events are unlikely to effect the relatively large southern England population significantly, this is certainly not the case in the early years in the midlands while the population is still small. An out-

break of disease in the midlands could wipe out the tiny breeding population completely by causing the deaths of only a handful of adult kites. This emphasizes the importance of ensuring that the vulnerable midlands population increases to a level at which such stochastic effects are less significant.

The model considered the impact of the translocation options on Red Kites in southern England and the midlands separately. However, given the stated aims of the project to reestablish the Red Kite throughout Britain, the translocation of birds should not be viewed as a loss to one area and a gain for another. In the long-term, translocated birds will form part of a single, larger British population. Although unrealistic, it is interesting to run the model for a longer period of time. If this is done for the southern England population under the "do nothing" scenario, then the population would reach 14 250 pairs in 2012 and 93 700 pairs by 2017. The population will clearly not reach such levels as quickly as predicted by the model because we can expect increasing competition among kites as the population expands in both numbers and range. This would likely increase age of first breeding, reduce levels of breeding productivity and reduce survival rates (Newton 1979), thus slowing the rate of population increase.

RESUMEN.—Un modelo determinístico simple fue utilizado para evaluar los resultados potenciales del traslado de *Milvus milvus* en Inglaterra como parte del proyecto de reintroducción de la English Nature/Royal Society for the Protection of Birds (RSPB). El modelo utilizó datos de sobrevivencia y productividad para el monitoreo de la población en expansión al sur de Inglaterra y demostró que el traslado de pequeños números de aves tienen poco efecto en esta población, pero si para la población de la región central. Dos escenarios incluyendo el traslado de distintos números de aves en períodos diferentes son presentados como ejemplos de como el modelo puede ser usado para evaluar las diferentes opciones. Al utilizar los resultados del modelo, la decisión fue la de trasladar los primeros 10 juveniles del sur de Inglaterra a la región central en 1997.

[Traducción de César Márquez]

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the Southern England Kite Group for helping to collect kite chicks for release in the midlands in 1997. The paper benefitted greatly from the comments of Dr. Ian Newton, Tom J. Cade and Harrison Tordoff.

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FIRST RECORDED POLYGYNOUS MATING IN THE RED KITE (*MILVUS MILVUS*)

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KEY WORDS: Red Kite, *Milvus milvus*; bigamy; polygyny; Doñana, Spain.

Diurnal birds of prey are predominantly monogamous (Newton 1979). Alternative mating systems like polygyny, polyandry, or cooperative breeding are rare, but have been recorded in at least 16 species of raptors (Newton 1979, Faaborg and Bednarz 1990, Heredia and Donazar 1990, Tella 1993, Tella et al. 1996). Nonmonogamous relationships are easily overlooked when working with unmarked individuals and are almost certainly more widespread than published records show (Newton 1979). Polygyny in birds of prey has only been regularly observed in harriers (*Circus* spp.) although it has been occasionally recorded in another nine species (Newton 1979, Hiraldo et al. 1991, Tella et al. 1996) and seems to

be associated with relatively productive habitats with an abundant food supply.

The Red Kite (*Milvus milvus*) is considered a monogamous raptor and to our knowledge no instances of polygyny have been reported previously (Glutz von Blotzheim et al. 1971, Newton 1979, Cramp and Simmons 1980). According to Glutz von Blotzheim et al. (1971) and Cramp and Simmons (1980), both adults build nests. Incubation is mainly done by females although males may incubate for short periods during the day. Males bring prey to females and defend nest sites during incubation and the first two weeks after hatching while females brood and feed the young. Later, both members of pairs defend nest sites and bring food to nests, where the young feed themselves. On average, young fledge 55 d after hatching and are fed by both parents for another 26 d in the vicinity of the nest (Bustamante 1993). The entire hunting territory is not defended, but Red Kites defend areas surrounding nest sites at least until the young become independent (Bustamante and Hiraldo 1993).

In 1996 and 1997, we recorded the presence of a po-

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lygynous trio of Red Kites in the area around the "Palacio de Doñana," Doñana Biological Reserve, southwest Spain (37°N, 6°30'W; Valverde 1958, Rogers and Myers 1980). The male could be identified by a white PVC band on the left leg with the code "2AU" that could be read with a telescope from approximately 200 m. This bird was banded as a nestling by L. García on 6 May 1977 in a pine forest named "Pinar de San Agustín," <1000 m from the "Palacio de Doñana." The bird was retrapped and observed several times during its life close to this pine forest and was documented breeding in this area at least since 1984 (B. Heredia, L. García, G. Vilchez, F. Hiraldo, M. Pineda and R. Lafitte pers. comm.). One female (F1) associated with this male was not banded and could only be identified due to her proximity to one of the nests. The other female (F2) using the territory had a metal band on the right leg, but we could not read this band. Due to the absence of differences in coloration or molting between the individuals, they could only be identified when they were perched in plain sight.

OBSERVATIONS IN 1996

Observations in March 1996 indicated that there was a polygynous trio in the area around the "Palacio de Doñana." On 8 March 1996, from 0757–1200 H, we were simultaneously observing what we thought were two different pairs of breeding Red Kites. One pair was observed building a nest in a stone pine (*Pinus pinea*) inside a small pine forest named "Pinar de San Agustín." One kite was banded with a white PVC band on the left leg that was read with the telescope as "2AU." The other kite (F1) was not banded. During observations, both kites were observed bringing material to the nest. On one occasion, they copulated indicating they were pair-bonded and we deduced "2AU" was the male and F1 the female. A second nest being observed was in a tall eucalyptus tree (*Eucalyptus globulus*) approximately 50 m east of the "Palacio de Doñana" and 800 m east of the first nest. Most of the time only one kite (F2) was observed in the area, flying and perching on the nest tree. This kite was banded with a metal band on the right leg. At 0934 H, a second kite, banded with white PVC band on the left leg, was seen perched 100 m from the nest. At 0959 and 1002 H, the kites copulated twice in another eucalyptus close to the nest tree. The copulation positions indicated that F2 was a female but we were not able to read the PVC band code of the male with a telescope. At 1005 H, the male with the white PVC band flew away. On 20 March 1996, F2 was observed copulating with the male with a white PVC band and both kites brought sticks to the nest in the eucalyptus tree. On 22 March 1996 at 1026 H, the nest was observed while F2 incubated. The male with the white PVC band flew to the nest and copulated with F2. On this occasion, the PVC band of the male was identified as "2AU." At 1234 H on the same day, a blind was set close to the nest occupied by F1 in the pine forest. At 1353 H, the male "2AU" entered the nest in the stone

pine with prey and began incubating. The male "2AU" was still incubating at 1415 H when observations were stopped.

The nest tended by F2 could be checked from an observation tower nearby. F2 laid one egg that failed to hatch for unknown reasons. We did not check the nest used by F1 until 8 May 1996. We found it contained two young that hatched on 20 and 21 April based on the length of their 7th primary feathers (Bustamante 1990). Both young fledged.

OBSERVATIONS IN 1997

We made opportunistic observations of the polygynous trio from 9 February–9 March. The male "2AU" was seen copulating with both an unbanded female on three occasions (9, 10, and 11 February) and a female with a metal band on the right leg on three occasions (13 February, 9 and 13 March). We suspect they were the same females, F1 and F2, from 1996. F1 was seen copulating and perched close to the male "2AU" in the same pine forest as in 1996 and F2 was seen bringing nest material to a nest in a poplar (*Populus alba*) 100 m north of the 1996 F2 nest. Only on one instance was the male seen bringing nest material to the pine forest nest. The F1 nest was located in a stone pine 50 m west from the 1996 nest. The distance between F1 and F2 nests was approximately 750 m.

Both nests were observed on a regular basis from 24 April–26 June, during which time the young of both nests grew from a few days old to fledging. Observations were carried out from a blind and were restricted to days that were mostly without clouds and low wind speeds to minimize the effects of weather conditions on the hunting success and feeding frequency of the kites. During this period, F1 nest was observed for a total of 33.4 hr on 11 different days ($\bar{x} = 3.0 \pm 2.0$ hr, \pm SD). F2 nest was observed for a total of 41.9 hr on 11 different days ($\bar{x} = 3.8 \pm 1.6$ hr, \pm SD).

The F1 nest contained two young that were banded on 30 April. We estimated that the young had hatched on 7 and 12 April. A total of 10 prey was observed delivered to the nest during 33.4 hr of observation; five were brought by the male "2AU," two by the female F1. In three instances, it was not possible to identify the individual bringing the prey. F2 nest contained one young that was banded on 17 May. We estimated hatching date to have been 24 April. We recorded eight prey delivered to the nest during 41.9 hr of observation and all were brought by the female F2. The male "2AU" was never seen at F2 nest. We approached both nests on several occasions. F1 nest was defended by two adults (kites hovering above the nest) while F2 nest was defended by only one kite.

DISCUSSION

Observations in 1996 clearly showed that the same male "2AU" copulated with two females that used differ-

ent nests, helped both females with nest building and helped one of them (F1) with incubation. Both females laid eggs and only one bred successfully. We cannot completely exclude from the 1996 observations that copulations with F2 were extra-pair copulations by "2AU" and that F2 may have had an undetected partner. Observations in 1997 were detailed enough to show that "2AU" was the only male seen with both females during nest building, incubation and brood rearing. The male "2AU" copulated seemingly equally with both females and helped both during nest building. During brood rearing, the male's attention was directed exclusively to the F1 female and F2 raised its single nestling alone.

Polygyny had not been previously documented in Red Kites, but as individuals tend to be very similar in coloration this behavior could be very easily overlooked unless kites are marked. This polygynous trio was similar to polygynous bondings observed in Northern Harriers (*Circus cyaneus*) (Simmons et al. 1986) in that there was a hierarchy between females. In the case of the Red Kites, the second female to lay eggs received no attention from the male once its young hatched. Nearest-neighbor distance between Red Kite nests (\bar{x} = 893.1 m, range = 690–2250, N = 21, Bustamante and Hiraldo 1990) was much shorter than elsewhere in Europe (4–5 km, Davies and Davis 1973, Valet 1975), probably indicating that there was abundant food for breeding Red Kites in Doñana. The Doñana area includes a highly productive marsh. The short distance between nesting territories in Doñana may have been a proximate cause facilitating this polygynous mating.

Four main hypotheses have been proposed to explain how polygyny may be advantageous. The "polygyny threshold" hypothesis (Verner and Wilson 1966, Orians 1969) suggests that a female should choose to mate polygynously in a high-quality territory when her fitness would be equal or greater than if she mated monogamously in a lower-quality territory. The "sexy son" hypothesis (Weatherhead and Robertson 1979) suggests that the female choice of polygyny could be based on the quality of the male rather than his territory. A third possibility is that if suitable breeding sites are limited and monopolized by a few males, females may be forced to mate polygynously rather than forgo breeding (Orians 1961). A skewed sex ratio (shortage of males) could be equivalent to limited breeding sites. Finally, the "deception" hypothesis (Alatalo et al. 1981) suggests that the male may be able to conceal its mated status to the females holding two separate territories.

It is difficult to believe that the male was able to deceive the second female and hide its mated status considering the polygynous trio was stable for two years and that the two nests were very close. In 1996 and 1997, we surveyed 32 nesting territories inside the Doñana Biological Reserve (10 000 ha) that had been occupied by Red Kites at least once since 1981. For the period 1981–97, the average number of nests in which Red Kites laid eggs

was 16 (maximum 19 nests). Red Kites laid eggs in 13 nests in 1996 and in 14 nests in 1997 (F. Hiraldo unpubl. data). Nesting sites did not seem to be limited in any of the two years. We do not know if there could be an unbalanced sex ratio or a lack of bachelor males. The territory of the male "2AU" could be of a higher quality than other territories in the area. The fact that F2 was able to raise a young in 1997 without the help of the male suggests that food was abundant in the proximity of the nest. The F2 nest was very close to a group of inhabited houses, the "Palacio de Doñana," that constitutes a predictable source of food for the kites. Also, we cannot exclude the possibility that the male "2AU" was of higher quality than other males. Male "2AU" was 19 years old in 1997, the oldest known-age Red Kite in our marked population (F. Hiraldo unpubl. data). The longevity of "2AU" may suggest this bird carried "good genes" and he may have been a high-quality male.

RESUMEN.—Se describen las observaciones de un trío poligínico de milanos reales (*Milvus milvus*) en la Reserva Biológica de Doñana, durante dos años consecutivos: 1996 y 1997. Un macho marcado, de edad conocida, se apareó con dos hembras, posiblemente las mismas ambos años, que utilizaron para poner nidos distintos. En 1996 la primera hembra crió dos pollos y la segunda fracasó. En 1997 la primera hembra en realizar la puesta crió dos pollos y la segunda uno. Se comprobó este año que el macho cebaba y defendía exclusivamente el nido de la primera hembra y que la segunda fue capaz de criar con éxito su pollo sin la ayuda del macho.

[Traducción de Autores]

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MITES IN GREATER SPOTTED EAGLE NESTS

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KEY WORDS: *Spotted Eagle*, *Aquila clanga*; mites; Acari; *Mesostigmata*; Biebrza National Park; Poland.

The Greater Spotted Eagle (*Aquila clanga*) is among the rarest predatory birds in the world, nesting from the eastern areas of Poland, through Belarus and Russia to the Pacific coast (Meyburg 1994). In Poland, it is legally protected and classified in the Red Data Book as Endangered (Król 1992). It nests in impenetrable boggy woods and, in Poland, only about 12 pairs remain in Biebrza National Park (Maciorowski et al. 1996). Greater Spotted Eagles build their nests only in birches (*Betula* spp.), black beech (*Alnus glutinosa*) and, less frequently, in oaks

(*Quercus* spp.) and willows (*Salix* spp.). While the mite fauna in the nests of several predatory birds has been studied in Europe (Nordberg 1936, Philips 1981, Wiśniewski and Hirschmann 1985, 1990, Mizera 1990, Mašan 1993), the acarofauna of Greater Spotted Eagle nests has never been described. In this paper, we identify mites of the order *Mesostigmata* which inhabit the nests of Greater Spotted Eagles in Poland. These mites are small (adult length 0.4–1.6 mm), free-living arachnids which have phoretic or other relationships with birds.

METHODS

Samples were obtained at two Greater Spotted Eagle nests in Biebrza National Park in northeastern Poland.

The lining of the first nest was collected in 1994. The sample contained branches and grass and weighed about 300 g. At the time of collection, there was one 7-wk-old nestling in the nest. Subsequent observation confirmed that this bird later successfully fledged. The nest was built in the crown of an aspen tree (*Populus tremuloides*) in 1991 and was reused each year. It was built mainly from branches and mistletoe. The sample from the second nest was collected in 1995. It had a similar composition and was approximately the same weight. This nest was in a birch tree.

Mites were extracted from collected material by funnel-heat dessication and preserved in 70% alcohol. For maceration and bleaching, mites were placed in a drop of lacto-phenol on a slide and a coverslip was applied. Permanent preparations were made in polyvinyl alcohol (Evans 1992).

RESULTS AND DISCUSSION

Only mites of the order *Mesostigmata* were identified to genus and species level. Two subclasses of mites were represented, the Anactinotrichida and Actinotrichida. In the subclass Anactinotrichida, we identified mites in seven families of the suborder Gamasina. Nest II contained one deutonymph of *Parasitus consanguineus* which is a rare species in the Parasitidae found in arable and meadow soils, in compost, stable manure, and in decomposing organic material (Karg 1993). This is a new species to the Polish fauna. We also found a Macrochelid, *Macrocheles ancyclus*, in both Nest I (104 females, 28 males, 21 deutonymphs, 9 protonymphs) and Nest II (242 females, 28 males, 15 deutonymphs, 5 protonymphs). It has been found previously in the decaying wood of aspen trees (Krauss 1970) but it is also a new species to the Polish fauna. Macrochelid mites are not uncommon in birds nests and are known from other raptor nests (Ambros et al. 1992, Philips et al. 1983, Zeman and Jurík 1981).

We also identified three species of mites in the family Ascidae: *Arctoseius cetratus*, *Proctolaelaps pini*, and *P. pygmaeus*. We found one female and one protonymph of *Arctoseius cetratus* in Nest I and two females in Nest II. This species has previously been found in soils of arable fields, in compost, in deciduous and mixed forests, and humus between plant roots (Karg 1993). In Nest II, we also found 37 females, seven males, nine deutonymphs, and five protonymphs of *P. pini*. It is typically found in pine stumps and on bark beetles (*Hylastes* spp.) (Karg 1993). We also found five females, one male, and one deutonymph of *P. pygmaeus* in Nest II. It has been previously found in soil, moss, decaying plants, and nests of small mammals (Bregetova 1977a).

Three species of mites were in the family Laelapidae. One female, one male, and one deutonymph of *Androlaelaps casalis* occurred in Nest II. It is a species typically found in the soils of meadows, humus between roots, hay and straw, and in nests of rodents and birds (Karg 1993), such as raptors (Philips 1981, Zeman and Jurík 1981). Also in Nest II, we found two females of *Hypoaspis* (*Cos-*

molaelaps) *vacua* which is typically encountered in deciduous and conifer forests, in humus and moss, in decaying wood, and in nests of ants of the genus *Lasius* (Bregetova 1977b, Karg 1993). Lastly, we identified two females of *Hypoaspis* (*Pneumolaelaps*) *lubrica* in Nest I. It is typically found on rotten plants, in rodent nests, and on rodents themselves, as well as in the nests of Sand Martins (*Riparia riparia*) (Karg 1993).

Three species in the family Digamasellidae occurred in both nests. A total of 40 females, four males, and 50 deutonymphs of *Dendrolaelaps* (*Punctodendrolaelaps*) *fallax* were in Nest I but only five females and one deutonymph were found in Nest II. This is a species that is commonly found in compost and stable manure (Hirschmann and Wiśniewski 1982, Karg 1993). Twelve female, one male, three deutonymph, and one larva of *Dendrolaelaps* (*Punctodendrolaelaps*) *wengrisae* were found in Nest II. It has been previously found in ant (*Formica fusca*) nests (Hirschmann and Wiśniewski 1982). Only one female of *Dendrolaelaps* (*Apophyseodendrolaelaps*) *zwoelferi* was in Nest II. It has been previously found in nests of the *Formica rufa*, under pine bark, in the pathways of *Dryocoetes autographus*, and in Sand Martin nests (Ščerbak 1980).

A female and a deutonymph of two additional species, *Paragarmania* sp. (Phytoseiidae) and *Halolaelaps* sp. (Halolaelapidae) were also found in Nest II.

We found mites representing five families in the suborder Uropodina. One species each in the families Trachytidae and Polyaspididae occurred in Nest I. We found one female *Trachytes aegrota* (Trachytidae). It is a species found in moss, soil, grass, often in litter of deciduous and conifer forests, in rotting wood, in the paths of bark beetles, in bird nests, nests of the mole *Talpa europaea*, and ant nests (Karg 1989, Wiśniewski and Hirschmann 1993). A total of 44 females, 49 males, 51 deutonymphs, 38 protonymphs, and one larva of *Uroseius* (*Apionoseius*) *infirmus* (Polyaspididae) were also identified from this nest. This species is typically found in moldy wood, in rotting parts of plants, in the litter of deciduous and coniferous forests, and in bird nests (Kadite and Petrova 1977, Karg 1989, Mašan 1993, Wiśniewski and Hirschmann 1993).

Three species in the family Trematuridae were in both nests but they were not common. A female and male of *Nenteria floralis*, a species associated with dunghills and greenhouse soils (Wiśniewski and Hirschmann 1993), were found in Nest II. This is a new species to the Polish fauna. Four females, three males, two deutonymphs, three protonymphs, and one larva of *Nenteria pandioni* were identified in Nest I and 74 females, 26 males, 229 deutonymphs, 48 protonymphs, and nine larvae were found in Nest II. This species has only been found in Osprey (*Pandion haliaetus*) and White-tailed Sea Eagle (*Haliaeetus albicilla*) nests (Wiśniewski and Hirschmann 1985, 1990) (Fig. 1). Two females of *Trichouropoda ovalis*, a species commonly found in hay, moss, mushrooms, straw, ant nests, the paths of *Scolytidae*, on *Cerambycidae* and *Scarabaeidae*, in decaying wood, in hollow tree trunks,

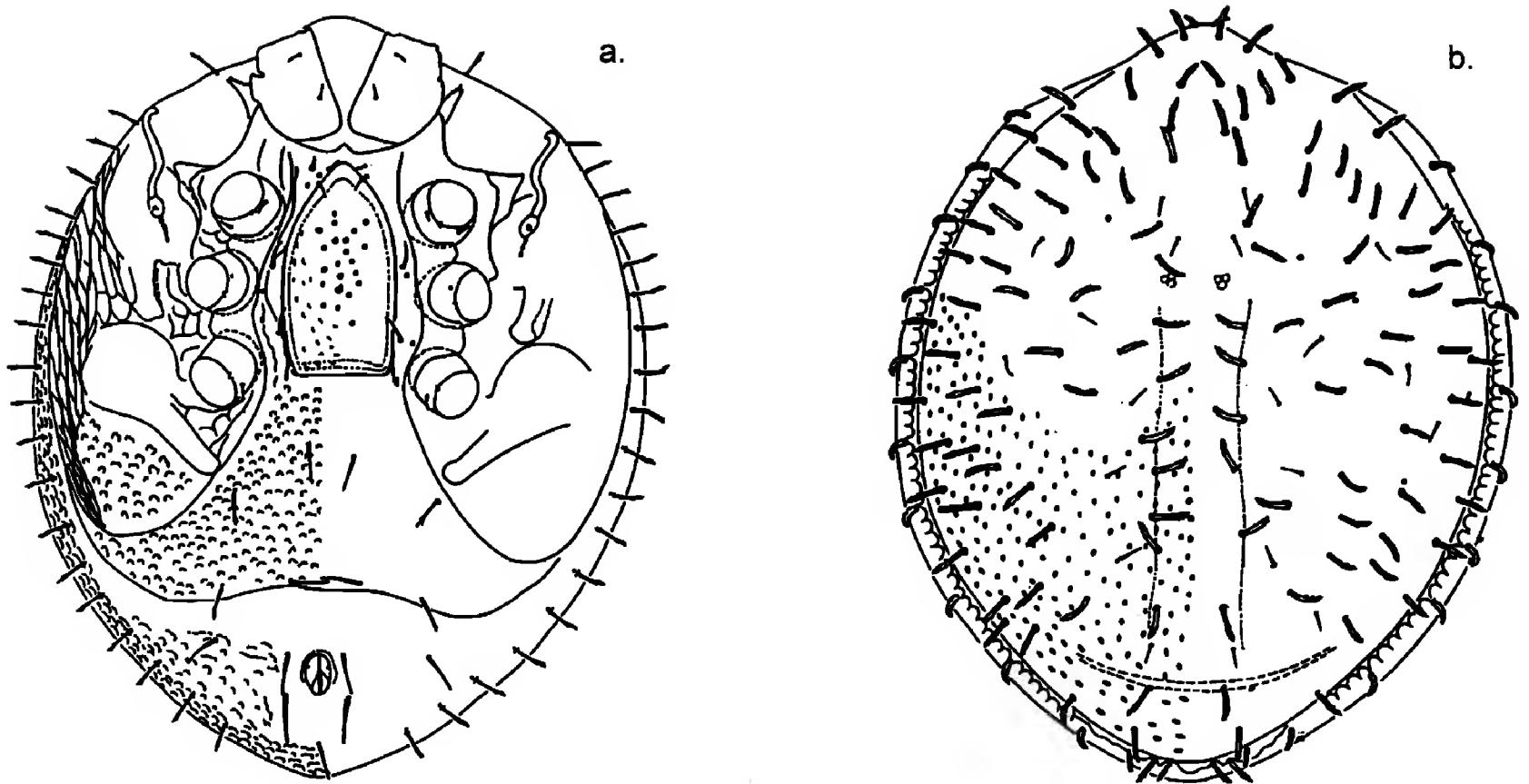


Figure 1. A dorsal view of *Nenteria pandioni* (Wiśniewski and Hirschmann 1985).

and in bird and mole nests (Wiśniewski and Hirschmann 1993), was also found in Nest II.

Two species of mites in the family Urodynychidae, *Dinychus perforatus* and *Uroobovella obovata*, were identified. One female of *Dinychus perforatus* was found in Nest I and *Uroobovella obovata* was found in both Nest I (two females, two males, and one deutonymph) and Nest II (seven females, three males, and two deutonymphs). Both species are usually encountered in rotting litter of deciduous forests, meadow soils, moss, decaying plant material, mole nests, and phoretically on birds (Karg 1989, Wiśniewski and Hirschmann 1993).

We found one representative of the family Uropodidae, *Uropoda* (*Phaulodinychus*) *hamulifera*. Ten deutonymphs and two protonymphs were found in both nests. This species is found in ant nests and stable manure (Karg 1989, Wiśniewski and Hirschmann 1993).

In the material collected, 1267 mites in the order Mesostigmata and 646 in the subclass Actinotrichida were found. Mites in the order Mesostigmata represented 21 species and 12 families. Eleven and 16 species of mites were found in Nests I and II, respectively. Six species were common to both nests. The most frequently found species in Nest I were *U. infirmus* (183 individuals), *M. ancyleus* (162), *D. fallax* (94), and *N. pandioni* (13). In Nest II, the most frequent species were *N. pandioni* (386), *M. ancyleus* (290), *P. pini* (58), and *D. wengrisae* (17). Species new to the Polish fauna were *M. ancyleus*, *N. floralis*, and *P. consanguineus*.

It is difficult to evaluate the relationship between free-living mites and predatory birds; however, some species of mites occur, almost exclusively, in nests of these birds.

Previously *N. pandioni* was found only in the nests of Ospreys and White-tailed Sea Eagles (Wiśniewski and Hirschmann 1985). The large numbers of all stages of development of *N. pandioni* that we found in Greater Spotted Eagle nests appear to confirm that eagle nests provide a specific microhabitat for this mite.

RESUMEN.—Los nidos de aves rapaces proveen un microhabitat para pequeños invertebrados, particularmente para piojos. Estudiamos la acarofauna del orden Mesostigmata que habita en nidos de *Aquila clanga* en el parque Nacional de Biebrza en el noreste de Polonia. Veintiuna especies de piojos fueron identificados. Una especie: *Nenteria pandioni*, aparentemente es dependiente del habitat de anidación de *Haliaeetus albicilla* y de *Pandion haliaetus*. Las otras especies fueron encontradas en madera podrida, basura, compost y nidos de aves.

[Traducción de César Márquez]

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FOOD HABITS OF THE RUFOUS-LEGGED OWL (*STRIX RUFIPES*) IN THE MEDITERRANEAN SCLEROPHYLLOUS FOREST OF CENTRAL CHILE

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KEY WORDS: *Rufous-legged Owl*; *Strix rufipes*; *food habits*; *Mediterranean sclerophyllous forest*; *central Chile*.

The Rufous-legged Owl (*Strix rufipes*) inhabits old-growth temperate rainforest of southern South America (Housse 1945, Goodall et al. 1946, Johnson 1967, Vuilleumier 1985, Martínez and Jaksic 1996, 1997). Infor-

mation on the species is limited, and only plumage, habitat and distribution have been described (Housse 1945, Goodall et al. 1946, Johnson 1967, Vuilleumier 1985, Araya and Millie 1989). Martínez (1993a, 1996) and Martínez and Jaksic (1996, 1997) have recently reported on population density, specific habitat requirements and diet of the Rufous-legged Owl in temperate rainforests of

southern Chile. They pointed out similarities in habitat requirements of this species and the Northern Spotted Owl (*Strix occidentalis*) of North America.

In Chile, the range of the Rufous-legged Owl extends from Santiago to Magallanes, (33°S–55°S) (Goodall et al. 1946, Araya and Millie 1989). In the northern limit of distribution, it inhabits hydrophyllous and sclerophyllous forest of the Mediterranean zone. Relative to southern Chile, abundance in central Chile is lower (Housse 1945, Jaksic and Jiménez 1986), and numbers appear to be declining as a result of habitat loss (Jaksic and Jiménez 1986).

From a conservation viewpoint, the Rufous-legged Owl has been catalogued as inadequately studied and in need of further research (Glade 1993). Historical records documenting the presence of Rufous-legged Owls in mountainous old-growth forest of central Chile (Housse 1945) date from the past century (specimens present at the National Museum of Natural History from Central Chile are MNHM 153 Aculeo 1865, MNHM 150 San Francisco del Monte 1869, MNHM 4338 Quebrada de Ramón 1947). Since the arrival of Spanish colonials, forests of the Central Valley and Andean range in Chile have largely been destroyed (Elizalde 1970, Mooney et al. 1972, Hoffmann 1998). During this century, forests near Santiago have virtually disappeared (Lara 1998), having been cut for firewood in Santiago and nearby towns. Trees older than 250 yr are scarce and may only be found along deep ravines in remote mountainous areas.

This study is the first report of the food habits of Rufous-legged Owl in the Mediterranean sclerophyllous forest near the northern limit of its distribution in Chile.

STUDY AREA AND METHODS

The study was conducted in Río Clarillo National Reserve (33°45'S, 70°26'W), located 45 km southeast of Santiago in the foothills of the Andean range. The reserve covers 10 185 ha of mountainous landscapes, with slopes of approximately $\geq 45^\circ$ and 870–3050 m in altitude (ICSA 1983). The climate at 870 m is Mediterranean with mean annual rainfall of 648 mm and a long dry season from September to May (CONAF 1996).

The reserve supports sclerophyllous forest <1500 m that are dominated by *Cryptocarya alba* (Lauraceae), *Persea lingue* (Lauraceae), *Drimys winteri* (Winteraceae), *Lithraea caustica* (Anacardiaceae), *Quillaja saponaria* (Rosaceae), and *Acacia caven* (Mimosaceae) (CONAF 1996, ICSA 1983). Between 1500–2000 m, *Kageneckia angustifolia* (Rosaceae) and *Austrocedrus chilensis* (Cupressaceae) are dominant. Above 2000 m, shrubs such as *Chuquiraga* sp. and *Mulinum* sp. grow to a height of 50 cm (ICSA 1983). According to local inhabitants, the location of the reserve was very remote until the middle of the century. However, around the turn of the century, the forest began to be exploited for firewood and charcoal, and open areas were used for cattle grazing during the summer (CONAF 1996, ICSA 1983). Exploitation was intensified in 1972, when indiscriminate tree removal began, and many parts of the reserve were burned and cleared

(CONAF 1996). In 1978, hunting was prohibited and, in 1982, the area was designated a national reserve (CONAF 1996, ICSA 1983).

A total of eight surveys were conducted on a periodic basis (one survey each two or three months) from February 1994–October 1995, in a forest patch less than 1 ha in size located at 1100 m altitude that was occupied by a Rufous-legged Owl pair. In all, 210 pellets were collected and their contents were identified to species level through comparisons with the mammal skull collection in the National Museum of Natural History, Santiago, Chile. A reference collection was also used to identify insects found in pellets. Data were pooled by season and the results expressed separately for each season as a percentage of the total prey mass consumed. The following equation was used to calculate the percentage of the total prey mass consumed represented by each species in the diet (Martínez 1993a), assuming that the entire body mass of each individual prey species caught was consumed by the owl:

$$B\% = (100Sp_iN_i) / \sum Sp_iN_i$$

where Sp_i is the mass of the i th species, N_i is the number of individuals of i th species consumed and $B\%$ is the percentage of the total prey mass consumed for each season contributed by the i th species. The mass of each prey species was obtained by capturing and weighing individuals of different taxa present in the Rufous-legged Owl diet. For mammals, body mass was obtained from Jaksic (1986).

RESULTS AND DISCUSSION

The diet of Rufous-legged Owl consisted of 10 mammalian species, one lizard and four invertebrate families (Table 1). In spite of the large number of invertebrates consumed, they composed only 2.1% of the total prey biomass. Mammals made up 98% of prey biomass in the Rufous-legged Owl diet (62% of the total of number of prey items consumed). The species most frequently consumed were *Abrocoma bennetti* and *Octodon lunatus*, comprising 16.5% and 15.2% of the total prey biomass, respectively. In addition, 29% of the prey biomass (13% of individual prey items identified) was attributed to mammals identified from remains retrieved from pellets which did not contain skulls or teeth. These pellets contained large femurs or humeri ($\bar{x} = 32.2 \pm 0.7$ and 27.6 ± 0.3 mm, respectively) identified as adult *A. bennetti* and *O. lunatus*, the only large rodents in the area (CONAF 1996, Díaz and Sarmiento 1999). These species constituted 35% of the total number of prey items identified, 51% of the mammals captured and the 61% of the total prey biomass consumed. Both are primarily terrestrial species which live in caves among rocks covered by shrubs (Mann 1978), and occasionally climb trees (C. Veloso pers. comm.). Lizards in central Chile are diurnal (Donoso-Barros 1966), and were probably consumed only occasionally.

In contrast to data presented by Martínez (1993a) and Martínez and Jaksic (1996, 1997) on Rufous-legged Owls in forests of southern Chile, prey species in this study

Table 1. Food habits of the Rufous-legged Owl (*Strix rufipes*) in sclerophyllous forest in Río Clarillo National Reserve, central Chile. Data from 1994 and 1995 are pooled by season. *B%* is a percent of total prey mass consumed and (*N*) is prey number by season.

PREY	Mass (g)	SUMMER		AUTUMN		WINTER		SPRING		TOTAL	
		B%	(N)	B%	(N)	B%	(N)	B%	(N)	B%	(N)
Mammals											
<i>Abrocoma bennetti</i>	219 ^a	30.0	(15)	20.0	(9)	0	(0)	14.0	(5)	19.0	(29)
<i>Abrocoma bennetti</i> *	169 ^b	6.2	(4)	1.8	(1)	27.0	(8)	4.2	(2)	7.5	(15)
<i>Octodon lunatus</i>	180 ^b	9.9	(6)	26.0	(14)	7.2	(2)	11.0	(5)	14.0	(27)
<i>Octodon lunatus</i> *	140 ^b	0	(0)	0	(0)	8.4	(3)	0	(0)	1.2	(3)
<i>Oryzomys longicaudatus</i>	45 ^a	0.4	(1)	1.9	(4)	1.8	(2)	5.0	(9)	2.1	(16)
<i>Abrothrix longipilis</i>	76 ^a	2.8	(4)	3.9	(5)	0	(0)	1.9	(2)	2.5	(11)
<i>Abrothrix olivaceus</i>	40 ^a	0.4	(1)	0.4	(1)	3.2	(4)	2.0	(4)	1.2	(10)
<i>Phyllotis darwini</i>	66 ^a	0.6	(1)	4.1	(6)	7.9	(6)	4.1	(5)	3.5	(18)
Cricetidae unident.	40 ^b	0.4	(1)	0.4	(1)	2.4	(3)	0.5	(1)	0.7	(6)
<i>Rattus norvegicus</i>	220	4.0	(2)	0	(0)	0	(0)	0	(0)	1.3	(2)
<i>Rattus rattus</i>	158 ^a	2.9	(2)	3.3	(2)	3.1	(1)	0	(0)	2.3	(5)
<i>Thylamys elegans</i>	40 ^a	2.2	(6)	2.9	(7)	3.2	(4)	3.0	(6)	2.7	(23)
<i>Oryctolagus cuniculus</i> *	408 ^b	7.5	(2)	0	(0)	16.0	(2)	0	(0)	4.9	(4)
Unident. large mammals	200 ^b	24.0	(13)	27.0	(13)	16.0	(4)	45.0	(18)	29.0	(48)
Unident. small mammals	58 ^b	6.4	(12)	5.4	(9)	2.3	(2)	7.9	(11)	5.9	(34)
Subtotal mammals		97.8	(70)	97.6	(72)	98.5	(41)	97.8	(68)	97.8	(251)
Reptilians											
Squamata unident.	10 ^b	0	(0)	0	(0)	0.2	(1)	0	(0)	0.03	(1)
Subtotal reptilians		0	(0)	0	(0)	0.2	(1)	0	(0)	0.03	(1)
Insects											
Cerambicidae											
<i>Acanthinodera cummingii</i>	11 ^b	1.1	(11)	0.6	(5)	0.4	(2)	0.7	(5)	0.8	(23)
Scarabeidae	0.3 ^b	0	(0)	0	(0)	0	(0)	0	(9)	0	(9)
Gryllacridiidae	3.2 ^b	0.4	(15)	1.7	(50)	0	(0)	0.8	(20)	0.8	(85)
Insecta unident.	4 ^b	0.6	(15)	0.1	(3)	0.9	(11)	0.7	(14)	0.5	(43)
Subtotal insects		2.1	(41)	2.4	(58)	1.3	(13)	2.2	(48)	2.1	(160)
Scorpions	0.8 ^b	0.1	(11)	0	(3)	0	(1)	0	(1)	0	(16)
Total prey items		122		133		56		117		428	
Total prey mass		10 882		9643		5025		8077		33 627	
Total pellets		59		55		29		67		210	

^a Prey biomass obtained from Jaksic (1986).
^b Prey biomass obtained from I. Díaz (unpubl. data).
* Young specimens.

were larger and primarily terrestrial. In southern Chile, 72.4% of the total prey mass consumed were scansorial mammals weighing 26–42 g (Martínez 1993a) while, in this study, adults of the dominant prey species, *A. bennetti* and *O. lunatus*, weighed between 180–219 g, and young individuals weighed over 100 g. In central Chile, *Abrothrix longipilis*, *A. olivaceus*, and *Oryzomys longicaudatus* made up a relatively small proportion of species consumed by Rufous-legged Owls, in contrast to southern Chile where they were consumed in large quantities (Martínez 1993a, Martínez and Jaksic 1996, 1997).

The sizes of prey species identified in this study are larger than the optimal prey size predicted by Bozinovic and Medel (1988) for owls of a similar size. Therefore, it is probable that individuals of Rufous-legged Owl did not select prey species according to optimal size, but according to prey species abundance. Large prey may have been eaten in pieces, instead of being swallowed whole. I have observed this behavior in Great Horned Owls (*Bubo virginianus*) when they caught and ate European rabbits (*Oryctolagus cuniculus*). Less palatable body parts or heads of large mammals which may have been too large to swal-

low may have been avoided. This could explain the high percentage of pellets found which did not contain teeth or skulls (Table 1).

The forest patch in Río Clarillo provided an open understory and forest floor which may have enhanced Rufous-legged Owls' ability to see and capture terrestrial mammals. The opposite is true in the southern Chilean rainforest, where dense understory provides cover for terrestrial mammals, and owls forage mainly on arboreal and scansorial mammals (Martínez 1993a, 1993b, Martínez and Jaksic 1997). In the Río Clarillo National Reserve forest patch, some *Persea lingue* and *Cryptocarya alba* trees are >200 years old and reach 13–15 m height. They provide 70% canopy cover, similar to that reported by Martínez and Jaksic (1996) in southern Chile. The Rufous-legged Owl pair studied in Río Clarillo was frequently observed outside forest patches during night hours, giving territorial vocalizations in open shrublands with a canopy <6 m in height. However, during the day they were always observed inside the forest patch and pellets were found only in the forest. It is my opinion that Rufous-legged Owls use forest patches for nesting and for protection and shelter during daylight hours, and forage in forest and shrublands during the night.

RESUMEN.—Este es el primer análisis cuantitativo de la dieta del Concón (*Strix rufipes*) en un bosque esclerófilo, cerca del límite norte de la distribución de esta especie en Chile. Se analizó el contenido de 210 egagrópilas recolectadas en un remanente de bosque esclerófilo entre 1994 y 1995. Los resultados indican que el Concón consumió mayoritariamente los roedores *Abrocoma bennetti* y *Octodon lunatus*, además de otras ocho especies de mamíferos, un lagarto y cuatro familias de artrópodos. El tamaño de las presas consumidas es de tres a cuatro veces mayor que el tamaño de las presas consumidas por esta misma especie en el sur de Chile. Las presas consumidas son fundamentalmente terrícolas, a diferencia de las especies arborícolas y escansoriales consumidas en el sur. Probablemente el Concón captura estas grandes presas y las consume por trozos. Se han detectado ejemplares fuera de los remanentes de bosque, en matorrales, por lo cual el Concón podría usar los bosques para descansar durante el día y anidar, y por la noche capturaría sus presas en bosques y matorrales vecinos.

[Traducción del Autor]

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FOOD HABITS OF THE CINEREOUS HARRIER (*CIRCUS CINEREUS*) IN THE ARAUCANÍA, SOUTHERN CHILE

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KEY WORDS: *Cinereous Harrier*, *Circus cinereus*; food; Chile.

The Cinereous Harrier (*Circus cinereus*) is widespread in South America, ranging from northern Colombia to Tierra del Fuego in open areas such as marshes, grasslands, shrublands, and steppes (Jiménez and Jaksic 1988, and references therein). In Chile, it is a resident along its entire distributional range from Copiapó (30°S) to Tierra del Fuego (57°S) (Hellmayr 1932, Johnson 1965). Its status varies from “rare” in northern Chile, to “frequent” in central and southern Chile, to “abundant” in southernmost Chile (Jaksic and Jiménez 1986). Although historical forest cutting and establishment of croplands has favorably affected the Cinereous Harrier in southern Chile, current increases of exotic pine and eucalyptus plantations and marsh draining for urban and agricultural development appear to negatively impact harriers by decreasing their hunting habitat, prey availability and nest sites (Jaksic and Jiménez 1986).

Little is known about the biology of this South American harrier, except for studies conducted by Jiménez and Jaksic (1988) in Chile and by Saggese and De Lucca (1995) in Argentina. Data on its diet in the Magellanic steppe were reported by Jiménez and Jaksic (1988) and

reanalyzed by Iriarte et al. (1990). Here, we report the first quantitative data on food habits of the Cinereous Harrier in an agricultural landscape of the Araucanía region (ca. 38°S) in southern Chile.

STUDY AREA AND METHODS

We studied two pairs of Cinereous Harriers in a 200-ha area at Tricauco Farm, located approximately 6 km south of Traiguén city (38°14'S, 72°38'W) in the Araucanía Region of Chile. The landscape comprised croplands of wheat and corn, grasslands, marshlands, exotic tree plantations of *Pinus* spp. and *Eucalyptus* spp. and remnants of the original deciduous *Nothofagus* forest. The climate is moist-temperate with a Mediterranean influence (di Castri and Hajek 1976) and mean annual rainfall and temperature are 1400 mm and 12°C, respectively. Although originally the Araucanía region extended from Maule Province to Seno Reloncaví, the current Administrative Araucanía Region extends from the Renaico River (37°30'S) to Calafquén Lake (38°47'S).

During August 1996 (austral winter), we collected 68 pellets in abandoned pastures and marshes where harriers hunted and perched. Pellets were collected both from open ground in pasture-marshes and under trees, fences and stumps used as perches by harriers. Avian prey were identified mainly on the basis of feathers, using two com-

Table 1. Food habits of Cinereous Harriers (*Circus cinereus*) in an agricultural landscape of the Araucanía, southern Chile.

PREY	MASS (g)	FREQUENCY (%)	BIOMASS (%)
Mammals		21.4	26.3
Rodentia			
<i>Abrothrix olivaceus</i>	23	4.4	0.9
<i>Oligoryzomys longicaudatus</i>	26	2.7	0.6
<i>Mus musculus</i>	21	0.9	0.2
Unidentified rodents	23	10.7	2.2
Lagomorpha			
<i>Oryctolagus cuniculus</i> ^{a,b}	800	0.9	6.4
<i>Lepus europaeus</i> ^{a,b}	1000	1.8	16.0
Birds		67.0	73.3
Tinamiformes			
<i>Nothoprocta perdicaria</i>	160	2.7	3.8
Ciconiiformes			
<i>Nycticorax nycticorax</i> ^a	600	0.9	4.8
Anseriformes			
<i>Anas flavirostris</i>	400	0.9	3.2
<i>Anas georgica</i>	700	1.8	11.2
Falconiformes			
<i>Milvago chimango</i> ^b	100	0.9	0.8
Galliformes			
<i>Callipepla californica</i> ^b	64	2.7	1.5
Charadriiformes			
<i>Vanellus chilensis</i>	270	3.5	8.6
Columbiformes			
<i>Columba araucana</i>	300	2.7	7.2
<i>Zenaida auriculata</i>	137	9.8	12.1
Passeriformes			
<i>Troglodytes aedon</i>	10	0.9	0.1
<i>Turdus falcklandii</i>	90	14.3	11.5
<i>Sicalis luteola</i>	16	15.2	2.2
<i>Sturnella loyca</i>	96	3.5	3.0
<i>Curaeus curaeus</i>	95	0.9	0.8
<i>Phrygilus patagonicus</i>	38	0.9	0.3
<i>Carduelis barbata</i>	15	0.9	0.1
Unident. passeriformes	51	4.5	2.0
Reptiles		4.5	0.3
<i>Liolaemus</i> spp.	8	4.5	0.3
Insects		7.1	0.03
Coleoptera	0.5	3.5	0.01
Orthoptera	0.5	1.8	0.01
Unident. insects	0.5	1.8	0.01
Total prey items (N)	112		
Total biomass (g)	12 502		
Total pellets (N)	68		

^a Likely juveniles.
^b Introduced.

plementary methods: microscopic analysis of feather structures such as nodes and barbules (Reyes 1992) and comparison of feather coloration patterns with voucher specimens deposited in the Zoology Department, Universidad Austral de Chile at Valdivia and in the National Museum of Natural History at Santiago. Because we observed harriers eating birds entirely, we used the presence of feathers of a given species in a pellet as representing only one individual. Mammals were identified and quantified on the basis of skulls or dentary pairs, whichever gave the highest count following keys in Reise (1973). Reptiles were identified and quantified by the presence of scales and/or teeth, and insects by head capsules, mandibles or elytra following keys in Donoso-Barros (1966) and Peña (1986), respectively. We identified prey items to the finest possible taxonomic category.

Biomass contribution was estimated following Marti (1987). Masses of birds and small mammals were obtained for birds using Jaksic et al. (1983), Morgado et al. (1987), Jiménez and Jaksic (1989) and Egli (1996) and for mammals using Greer (1968), Pearson (1983) and Martínez (1993). Masses of lagomorphs were obtained from juveniles found killed by raptors such as Cinereous Harriers and Short-eared Owls (*Asio flammeus*). Masses of lizards and insects were obtained from unpublished data of the authors. We assumed that masses of unidentified prey were similar to the mean mass of the most closely related identified taxon.

Although it was not possible to obtain simultaneous data on relative abundance of bird species, during the winter of 1997 we estimated bird abundance using eight parallel, fixed-band (100 m wide) line transects (Bibby et al. 1993) placed 400 m apart in the hunting areas of harriers. To test whether harriers took birds selectively or opportunistically, we compared prey frequency distribution in pellets with bird abundance using Spearman's rank correlations as recommended by Jaksic (1979) for coarse comparisons between prey consumption and availability.

RESULTS AND DISCUSSION

Pellets averaged 28.2 ± 1.9 (\pm SE) mm in length and 14.9 ± 0.9 mm in width ($N = 50$) and had a mean dry weight of 1.0 ± 0.6 g ($N = 68$). We identified 112 prey items in these pellets including 16 species of birds, five species of mammals, one species of reptile and two orders of insects. Birds were the staple prey comprising 67% by frequency and 73% by biomass of the diet. Most birds eaten were Passeriformes (41.1%) with Grassland Yellow-Finches (*Sicalis luteola*) and Austral Thrushes (*Turdus falcklandii*) being the most frequently eaten (Table 1). Eared Doves (*Zenaidura macroura*) ranked third by frequency but, by biomass, Eared Doves and Austral Thrushes were the most important prey. This agreed with anecdotal reports by Housse (1945), who indicated that Eared Doves were the preferred prey of Cinereous Harriers in southcentral Chile. Mammals were the second most common prey with olivaceous field mice (*Abrothrix olivacea*) and long-tailed rice rats (*Oligoryzomys longicaudatus*) the most frequent. However, because of their larger size, lagomorphs accounted for almost all of the mam-

malian biomass (22.4%). The incidence of reptiles and insects was negligible both by number and biomass.

Spearman rank correlation coefficients were $r_s = 0.72$ ($P < 0.01$) when all bird prey species were considered, and $r_s = 0.94$ ($P = 0.02$) when passerines alone were considered. These trends indicated that Cinereous Harriers hunted avian prey opportunistically rather than selectively (i.e., they took avian prey in proportion to their availability).

Overall, our results agree with those of Jiménez and Jaksic (1988), who reported that birds were the main prey of Cinereous Harriers during the breeding season in steppe marshes of Magallanes, southernmost Chile. Also, the diet of these harriers was similar to that of Long-winged Harriers (*Circus buffoni*) in Argentina (Bó et al. 1996), indicating that South American harriers are essentially bird predators.

RESUMEN.—Determinamos la dieta del vari (*Circus cinereus*) en agroecosistemas de la Región de la Araucanía, sur de Chile, analizando 68 egagrópilas colectadas en asociaciones de pastizal-humedal durante el invierno de 1996. Los varis consumieron un amplio espectro de presas que incluyó aves, mamíferos, reptiles e insectos. Sin embargo, las aves fueron la base de la dieta (16 especies presa), alcanzando 67% en frecuencia y 73% en biomasa. Entre éstas, las más frecuentes fueron *Sicalis luteola* (15%), *Turdus falcklandii* (14%) y *Zenaida auriculata* (10%). En términos de biomasa, *Z. auriculata* y *T. falcklandii* hicieron una mayor contribución a la dieta (ca. 12% cada uno). Los mamíferos alcanzaron el 21% de la frecuencia y contribuyeron con el 26% de la biomasa. La contribución de reptiles e insectos fue poco relevante. En general, nuestros resultados son coincidentes con otros autores, quienes mencionan a las aves como las principales presas de los varis en la Región de Magallanes.

[Traducción de Autores]

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STRIATED CARACARA (*PHALCOBOENUS AUSTRALIS*) POPULATION AT STATEN AND AÑO NUEVO ISLANDS

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KEY WORDS: *Striated Caracara*; *Phalcoboenus australis*; *population size*, *Argentina*.

The Striated Caracara (*Phalcoboenus australis*) is currently considered to be globally Near-threatened (Collar et al. 1994). Distributed on southern islands off southern South America (Narosky and Yzurieta 1987), its heavy persecution on the Islas Malvinas (Falkland Islands), where it was believed to attack weak or stranded sheep (del Hoyo et al. 1994), led to its local extinction and isolation on the smaller islands of the group. Its present status is currently unknown and surveys are needed, especially in the islands where Striated Caracaras are supposedly locally numerous (del Hoyo et al. 1994). Here, we report on the first exhaustive Striated Caracara census conducted at Staten and Año Nuevo islands during a scientific survey aimed at evaluating the islands' faunal conservation status (Parera et al. 1997).

Both islands (63 000 ha) are located at the southern extreme of South America, 30 km away from Isla Grande de Tierra del Fuego which is shared by both Argentina and Chile across the Le Maire Straits (Fig. 1). The topography of Staten Island is rugged with a peak elevation of 823 m at Monte Bove and the coastline is highly irregular with many fiords and bays (Kühnemann 1976). The Año Nuevo Islands are a group of islets with similar topography, north of Staten Island. The weather on both islands is cold with a mean temperature of 6–8 and –2–4°C during summer and winter, respectively. Oceanic humid winds are responsible for an annual rainfall of 2000 mm (Kühnemann 1976).

The survey was conducted from 12 November–9 December 1995. Counts were conducted by three experienced observers from a 12-m long sailboat (maximum 110 m off the coastline), a rubber boat and ground searching by foot when possible. Binoculars (10×50) and a 12–40× spotting scope were used for bird identification. The position of detected birds was obtained with a Global Positioning System (Garmin 50, GPS).

Thirty-seven different Striated Caracaras were observed at 12 locations along 196 km of coastline survey (68% of total island coastline, Fig. 1) for a linear density of one caracara for every 5.3 km. Two Andean Condors (*Vultur gryphus*), 17 Turkey Vultures (*Cathartes aura*), one Grey Buzzard-Eagle (*Geranoaetus melanoleucus*), six Crested Ca-

racaras (*Caracara plancus*), and one Red-backed Hawk (*Buteo polyosoma*) were also observed during surveys. Striated Caracaras were the most abundant raptors accounting for 59% of total observations and were as common as Crested Caracaras in continental habitats (one individual for every 4.4 km; Travaini et al. 1995).

Crested Caracara and Turkey Vulture counts at Staten Island were similar to those obtained for the same species in Patagonia where linear densities were 40 and 14 km/individual, respectively (Travaini et al. 1995). Relative abundances for the other three raptor species we observed were quite low when compared to figures obtained in continental Patagonia where linear densities of Andean Condors, Grey Buzzard-Eagles, and Red-backed Hawks ranged between 40–60 km/individual (Donazar et al. 1993).

Striated Caracaras were more abundant in our study area than in the Peninsula Mitre in Tierra del Fuego (Clark 1984). All the Striated Caracaras we observed were at or in close proximity to colonies of marine mammals and seabirds. We observed 68 seabird and marine mammal colonies along 196 km of coastline at Staten and Año Nuevo Islands compared to only 12 colonies along 170 km of coastline at Peninsula Mitre, Tierra del Fuego (Parera et al. 1997, Schiavini unpubl. data). Differential availability of food sources could explain the higher abundance of Striated Caracaras. Staten and Año Nuevo Islands should be considered key areas to protect this geographically isolated raptorial species.

RESUMEN.—Aunque el estado de conservación del Carancho austral (*Phalcoboenus australis*) se considera incierto, la fuerte persecución de sus poblaciones por el hombre hace suponer que podría estar amenazada. Aquí describimos los resultados de un censo realizado para esta especie en Isla de los Estados e Islas de Año Nuevo (54°45'S, 64°98'W). Sobre un recorrido de 196 km, el 68% de la línea de costa total de las islas, se contaron 37 caranchos australes (un individuo cada 5.3 km). El carancho austral resultó ser la rapaz más abundante del área estudiada, alcanzando sus densidades valores similares al de poblaciones bien conservadas del Carancho común (*Caracara plancus*) en áreas continentales. La abundancia del Carancho austral registrada en nuestro estudio es de las más altas descritas para esta especie. La cantidad de colonias de aves y mamíferos marinos presentes en las islas y la fuerte asociación de la es-

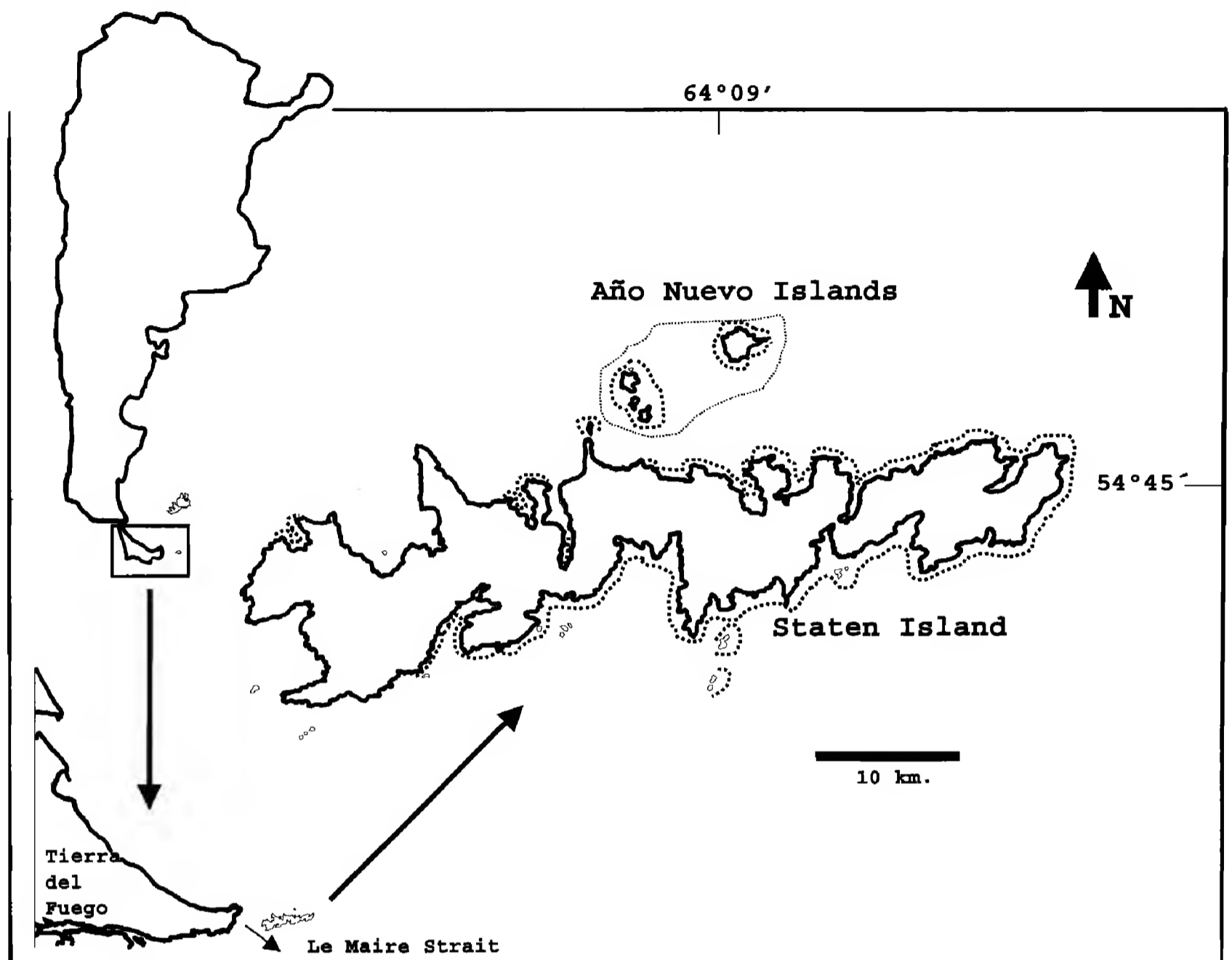


Figure 1. The location of Staten and Año Nuevo Islands. The dotted line shows the coastline that was surveyed.

pecie con estas colonias, parecen ser las causas del buen estado de conservación de la población de Carancho austral. Isla del los estados e Islas de Año Nuevo deben ser consideradas como áreas prioritarias para la conservación de esta especie.

[Traducción de Autores]

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LETTERS

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FORAGING OF YELLOW-HEADED CARACARAS IN THE FUR OF A THREE-TOED SLOTH

Both the Yellow-headed Caracara (*Mitvago chimachima*) and the brown-throated three-toed sloth (*Bradypus variegatus*) inhabit low elevation areas from southern Central America to northern Argentina (Emmons 1990, Neotropical rainforest mammals: a field guide. Univ. Chicago Press, Chicago, IL U.S.A.; Sick 1993, Birds in Brazil, a natural history. Princeton Univ. Press, Princeton, NJ U.S.A.). The sloth is generally limited to forested environments (Emmons 1990), while the caracara prefers more open habitat (Haverschmidt 1962, *Condor* 64:154–158; Sick 1993). Under natural circumstances, most interactions between these two species should be limited to forest edges. In metropolitan settings, however, species may be forced together in parks encircled by urban surroundings. In these situations, it may be easier to observe behaviors between species that remain undetected in more remote areas. Here, we describe the foraging on a brown-throated three-toed sloth by Yellow-headed Caracaras.

We observed the animals in the botanical garden of the Ciudad Universitaria in downtown Caracas, Venezuela, at approximately 1600 H on 16 November 1996. The sloth was 15–20 m above the ground in an isolated *Cecropia* tree, and was attended by two juvenile caracaras. The caracaras appeared to be picking from the fur of the sloth; our observational distance precluded us from seeing anything in the birds' beaks. The sloth showed no sign of defensiveness or aggression toward the caracaras even when they were foraging on its head and neck. It assumed a relaxed posture, reclining on a branch with its front legs extended behind its head. The behavior continued for 5–10 min, until we moved closer. At this point, the caracaras stopped their grooming behavior but remained within a few meters of the sloth. The caracaras appeared to be members of a larger group; we observed an adult and another juvenile in nearby trees.

Although previously undescribed, the nature of this interaction is not surprising. Yellow-headed Caracaras are known to forage by picking ticks and botflies from domestic livestock. When no source of appropriate ectoparasites is available, caracaras are opportunistic and may consume a wide variety of items including insects, fruit and carrion (Haverschmidt 1962). Thus, their opportunistic foraging in the fur of other slow-moving mammals may not be entirely unexpected. Sloths may represent a particularly attractive foraging substrate, as their fur contains a rich fauna of invertebrates, especially Lepidoptera (Waage and Montgomery 1976, *Science* 193:157–158).

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COMMON BLACK-HAWK NESTING IN WEST-CENTRAL TEXAS

Common Black-Hawks (*Buteogallus anthracinus*) are obligate riparian nesters of the southwestern U.S. Although not federally listed, it is listed as Endangered in New Mexico and Threatened in Texas (Schnell 1994, Common Black-Hawk, Birds of North America, No. 122, A. Poole and F. Gill [Eds.], The Birds of North America, Inc., Philadelphia, PA U.S.A.). Once a regular nester along the lower Rio Grande Valley of Texas, all local breeders were extirpated by 1940, apparently the result of extensive habitat loss. In 1970, a small breeding population (about 10 pairs) was discovered along Lympia Creek of the Davis Mountains in Jeff Davis County, Texas (Oberholser 1974, The bird life of Texas. Vol. 1., Univ. Texas Press, Austin, TX U.S.A.; Schnell 1994). To date, this remains the only known regular

breeding population in Texas. Extralimital breeding attempts have been reported in Val Verde (Lasley and Sexton 1988, *Am. Birds* 42:456–462), Lubbock (Texas Ornithological Society 1995, Checklist of Texas birds, Capital Printing, Inc., Austin, TX U.S.A.), and Brewster (Lasley and Lockwood, Texas Bird Records Committee, Texas Ornithological Society, pers. comm.) counties and the lower Rio Grande Valley (Webster 1976, *Am. Birds* 23:975–978). Only in the Davis Mountains has successful breeding been documented for consecutive years. Nesting attempts by a Common Black-Hawk pair in Big Bend National Park, Brewster County, Texas, were unsuccessful in 1997 and 1998 (M. Lockwood pers. comm.).

We observed the successful nesting of a pair of Common Black-Hawks in Tom Green County, Texas from 1996–98, at a location 345 km northeast of the nearest breeding population at Lympia Creek. A single pair of Common Black-Hawks was initially found during June 1996 nesting in a narrow (<300 m wide) band of riparian woodland along the spring-fed Cole Creek, a tributary of the South Concho River (2.5 km south, 0.62 km west Christoval, Texas). The 67 ha riparian woodland was dominated by pecan trees (*Carya illinoensis*; 49%), bur oak (*Quercus macrocarpa*; 14%) and plateau liveoak (*Q. virginiana*; 7%). Seven other tree species were present, but in small numbers. Mean tree density and mean canopy height, as determined by a point-quarter technique (Cottam and Curtis 1956, *Ecology* 37:451–460), was 383 ha⁻¹ and 21.4 m, respectively. Adjacent vegetation consisted of a patchwork of mixed mesquite (*Prosopis glandulosa*) brushlands and juniper (*Juniperus* spp.)-liveoak savanna. When they were found, the adults were carrying food (an unidentified snake) back to a nest containing one nestling. The nest was in the forked primary limb of a pecan tree of greater than local average size. The nest tree was 26 m tall, had a dbh of 107.7 cm and a maximum canopy width of 14.6 m. It was positioned 78 m from the edge of the riparian woodland and 125 m from Cole Creek. The closest tree of equal or greater dbh was 103 m away. Before nest measurements could be taken, the limb holding the nest fell during a storm following fledging. In 1997, a nest was constructed in the fork of a primary limb of the same pecan tree at a height of 18 m and 4.5 m from canopy edge. The limb had an estimated diameter of 26 cm at the base of the fork; the three branches arising from the fork had a diameter of about 14 cm. This same nest was subsequently reused in 1998.

Irregular visits were made to the site throughout the summer of 1996 and again from April through August of 1997 and 1998. During 1997 and 1998, a pair was observed nesting in the same tree as 1996. We observed the successful fledging of one individual each year. Attempts to band adults were unsuccessful, so we do not know if the nesting pair was the same each year.

Although the nest was close to water in Cole Creek (125 m away), all foraging we observed was from the South Concho River at a man-made rock dam (1 km away). We were unable to identify food items carried from the South Concho River, but potential prey observed at the rock dam included crayfish (*Procambarus clarkii*), largemouth bass (*Micropterus salmoides*), gizzard shad (*Dorosoma cepedianum*), channel (*Ictalurus punctatus*), blue (*I. furcatus*) and flathead (*Pylodictis olivaris*) catfish, green (*Lepomis cyanellus*) and long-eared (*L. megalotis*) sunfish, bluegill (*L. macrochirus*), Rio Grande (*Rana berlandieri*) and plains (*R. blairi*) leopard frogs, cricket frog (*Acris crepitans*), checkered garter snake (*Thamnophis marcianus*), ribbon snake (*T. proximus*), plain-bellied (*Nerodia erythrogaster*) and diamond-backed (*N. rhombifera*) watersnakes, and cottonmouth (*Agkistrodon piscivorus*).

While local tree species composition can be considerably different, structural characteristics of this location were similar to those reported at other nesting sites in Arizona, New Mexico and Texas (Schnell 1994). It is the isolation and consistent breeding success at this location that makes these records important. To our knowledge, this is the first known incident of successful breeding of Common Black-Hawks outside of the Davis Mountains in Texas since 1939. The chance discovery of this nesting site brings up the issue of potential range expansion by a species considered Threatened in Texas. While similar pockets of riparian woodlands are widespread in west-central Texas, potentially providing suitable nesting habitat, many of these sites are on private land holdings making extensive surveys for more nests difficult.

We thank the Boulware family for generously allowing us continued access to the nesting site and the summer 1998 Ecology class at Angelo State University for collecting local vegetation data. We also thank J.H. Schnell, R. Glinski and P. Bloom for helpful comments on earlier versions of this manuscript.—**Terry C. Maxwell, Department of Biology, Angelo State University, San Angelo, Texas 76909 U.S.A. and Michael S. Husak, Department of Biological Sciences, Mississippi State University, Mississippi State, Mississippi 39762 U.S.A.**

BOOK REVIEW

EDITED BY JEFFREY S. MARKS

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Holarctic Birds of Prey. Edited by B.-U. Meyburg, R.D. Chancellor, and J.J. Ferrero. 1998. World Working Group on Birds of Prey and Owls, Berlin, Germany. 680 pp., numerous figures and tables. ISBN 84-605-7398-2. Paper, \$35.—In conjunction with ADENEX (Asociación para la Defensa de la Naturaleza y los Recursos de Extremadura), the World Working Group on Birds of Prey and Owls (WWGBP) held a conference in Badajoz, Spain, from 17–22 April 1995. Of the 100 or so oral and poster presentations, 59 are included in this proceedings (16 in Spanish, 43 in English), which is organized into eight parts: “Molecular Systematics of Holarctic Birds of Prey and Owls” (3 papers), “Breeding Biology of Raptors” (7), “Biology and Conservation of Diurnal Raptors” (26), “Supporting Raptor Populations in Danger of Extinction via Captive Breeding” (4), “Biology and Conservation of Holarctic Owls” (5), “Raptors: Contamination and Development” (4), “Socio-economic Aspects of Raptor Conservation” (3), and “Migration of Birds of Prey” (7). Rather than attempt to mention all of the papers, I will note a few (among the many) that I found to be especially interesting.

Papers by Michael Wink and associates present data on molecular systematics of hawks and owls based on the cytochrome-*b* gene. The latter paper (with P. Heidrich) contains two notable tidbits: (1) the genetic distance is 5–7% between Little Owls (*Athene noctua*) from Israel versus Europe, suggesting that two species are involved; and (2) the “white-faced scops-owls,” formerly regarded as two taxa of *Otus*, actually are closer to *Asio* and belong in the genus *Ptilopsis*.

Among the handful of contributions from North America, Charles Henny presents a review of chemical contamination that focuses on falconi-

forms, James Enderson et al. provide an overview of the captive-breeding program for Peregrine Falcons (*Falco peregrinus*) in the U.S.A. and Canada, and Keith Bildstein challenges raptor biologists who study migration to form partnerships with mainstream ecologists and conservation biologists to broaden efforts to understand raptor migration on a global scale. Another thought-provoking paper, by Clayton White and Lloyd Kiff, discusses how efforts to list the Northern Goshawk (*Accipiter gentilis*) and to avoid delisting the Peregrine Falcon potentially weaken the Endangered Species Act by clouding the definition of “endangered” and by lowering the credibility of biologists who study these species. This paper should be read by everyone interested in the conservation of rare and threatened species.

Jeff Watson reports that Golden Eagles (*Aquila chrysaetos*) in western Scotland take a higher diversity of prey species than those in eastern Scotland and have concomitantly lower reproductive success. The difference in diet results from reduced numbers of medium-sized herbivores in western Scotland. Watson suggests that Golden Eagles do best when a few species of prey of favored size are “particularly abundant” and that they fair poorly when forced to widen their diet to include species outside of the preferred range of prey size. Ian Newton reviews migration patterns of falconiforms in the western Palearctic, drawing a correlation between migration distance and diet. Raptors that specialize on birds and mammals tend to migrate short distances and winter in the Palearctic, whereas those that eat mainly cold-blooded prey (i.e., reptiles and invertebrates) are long-distance migrants that winter in sub-Saharan Africa.

Holarctic Birds of Prey continues the line of worthwhile publications on raptor biology edited by Chancellor, Meyburg, and their associates and produced by the WWGBP. As such, it would make a valuable addition to one’s library.—**Jeff Marks, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812 U.S.A.**

ERRATUM

J. Raptor Res. 33(3):273

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DIET COMPOSITION AND REPRODUCTIVE SUCCESS OF MEXICAN SPOTTED OWLS

The following correction should be made to the article "Diet Composition and Reproductive Success of Mexican Spotted Owls," *Journal of Raptor Research* 33(2):143–148.

Page 143, abstract, third sentence of abstract should read "This was contrary to previously observed diet patterns in Northern (*S. o. caurina*) and California Spotted Owls (*S. o. occidentalis*). Mammals comprised 88.2% of the dietary biomass in Arizona and 94.0% in New Mexico."

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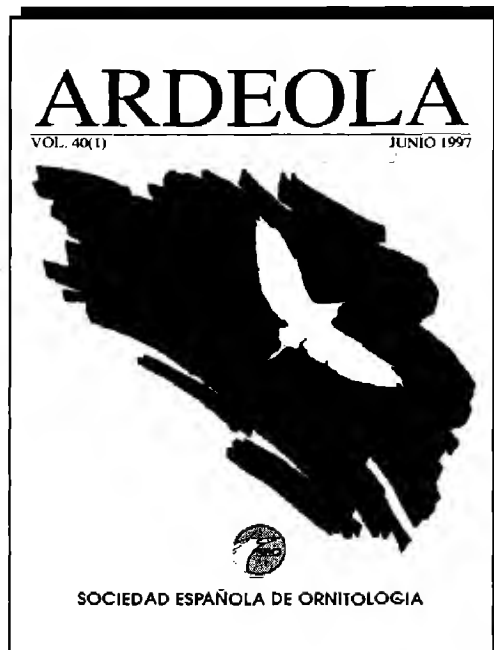
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